

# INTRODUCTION TO THE BOTANY OF FIELD CROPS

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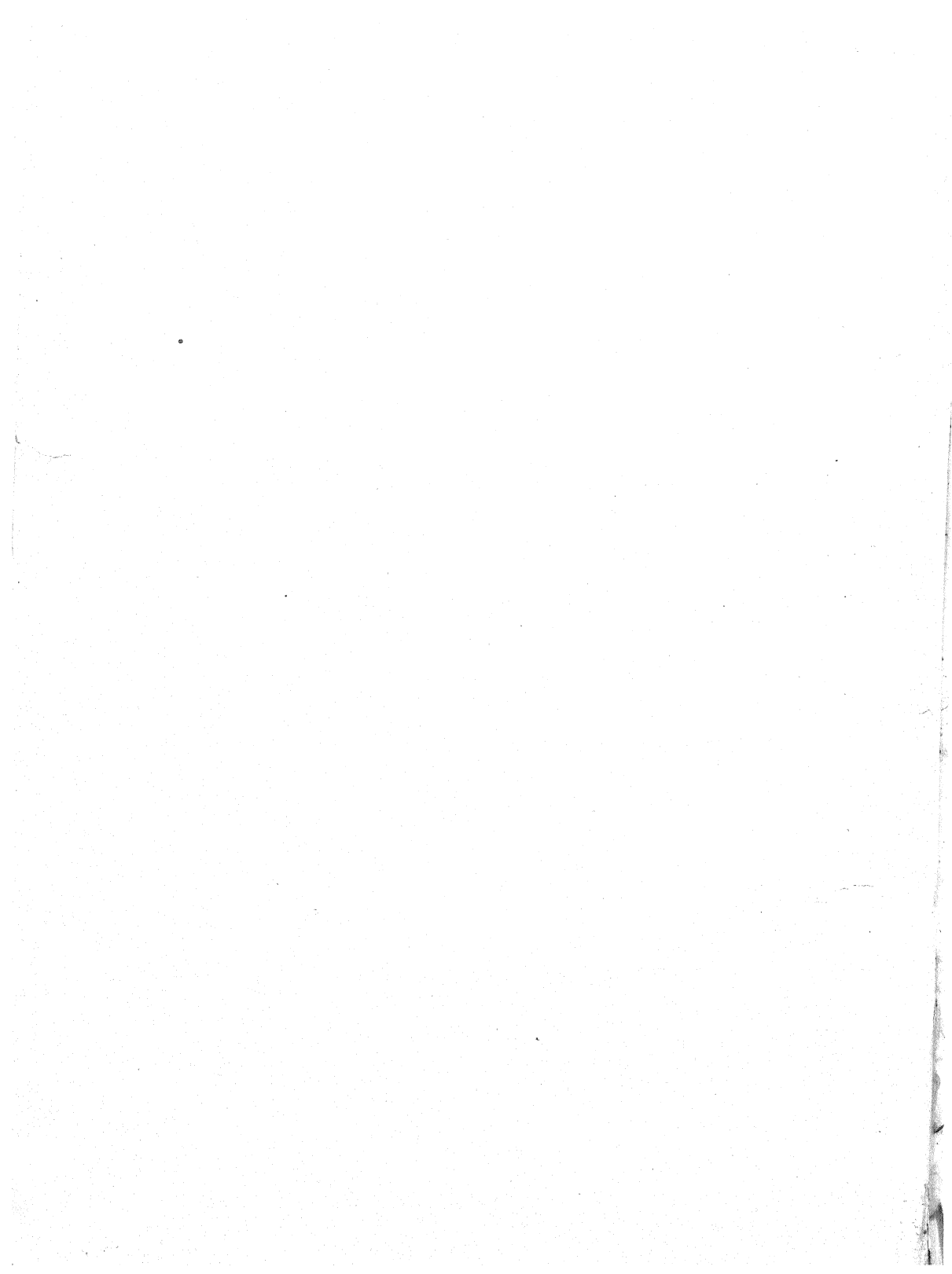
To  
THE MEMORY OF  
MY FATHER:  
AND TO MY STUDENTS, PAST AND PRESENT



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## PREFACE

THE term "field crops" is here used in a particulate sense: inclusively to incorporate all plants cultivated in the "field," *i.e.*, on arable land; exclusively to omit the plants of the garden, the orchard, the grove and the plantation. The distinction, however, is not absolute, since all "cultivated" grasses are omitted and certain plants, such as cotton—regarded in certain areas as a "plantation crop"—are included.

Since 1900, our knowledge of the botany of cultivated plants has increased enormously. New aspects of their study have developed. The literature has become not only extensive but very varied and widely scattered. As a consequence, the necessity for a co-ordinated account has become ever more manifest. In this text I have attempted to meet the need.

The book has not been written merely as a "text book" in the accepted meaning of the term; nor does its subject matter "fit" any particular course. Given a basic knowledge of elementary botany, the student—provided he simultaneously expands his knowledge along certain lines—could use the text throughout his curriculum.

To the post-graduate student, the investigator—now often confined to the study of but one plant or group of plants—and to the teacher, the book should also prove of value. If, however, the book has the requirements of any particular class of student in view, it is those of the senior and post-graduate student in particular, whether he be labelled "Botanist" or "Agronomist." But to all such it is an "introduction" to a study which is rapidly expanding, adopting new viewpoints and modes of approach, tentative and dynamic; an "introduction" to its literature, comprehensive perhaps, but in no sense exhaustive; a beginning, in brief, and not an end.

Much of the material might also be used as a basis for an introductory course in Botany. Indeed our knowledge of certain crop plants, *e.g.*, wheat and maize, some of the cruciferae, the beet plant, certain legumes, the potato, tobacco and cotton—is now far more detailed than that of any other species or genus. Yet in courses of "pure botany" they are largely ignored!

The scope of the text is also limited. I have not attempted to give complete genetical analyses; the importance of the cytological approach is, I believe, made obvious but not over-emphasised; physiological aspects are dealt with only incidentally—the individual treatment adopted practically forbids it—yet in certain chapters the value of physiological studies as a method has been stressed. One aspect, however, has been omitted—the viewpoint now generally known as "crop ecology." Here knowledge is, I feel, too vague at present for generalization. As a consequence, "tit-bits" such as "grows best in a deep loam" have found no place.

In re-reading the text, I find it wellnigh impossible to discriminate between what is due to my personal knowledge—the observations of over twenty-five years—and to that of the many investigators who have contributed to the subject matter. Nevertheless, I have striven, wherever possible, to acknowledge the original

authority. The author's name in the text with the date of publication in brackets has been employed throughout. Where a name (or names) occurs at the end of a section, it indicates that the preceding text is based mainly on the publication (or publications) of the investigator (or investigators) concerned.

Inevitably, I fear, there must be many omissions and faulty references. In extenuation of these errors I would point out that the subject-matter of the book covers a fairly wide field, and that there is marked difficulty in obtaining certain literature in the Union of South Africa. Misrepresentation or unfair criticism of the work of others no doubt also occurs; such errors are unwitting; my endeavour throughout has been to be fair, accurate and impartial. I should, however, be glad to receive criticism, and if a second edition of the text be published, will not hesitate to amend and rectify. It should, however, be noted that no attempt has been made to deal adequately with the literature of 1936.

In the preparation of the book I have many obligations to acknowledge. In the first instance, my indebtedness to my colleague, Miss E. E. Wyers, is outstanding. She has assisted in every phase of its compilation from the first drafts to the final proofs. I regard her indeed as the co-author of this book: only her firm refusal has prevented me putting her name on the title page.

The chapter on "Cotton" was read critically by Mr. O. V. S. Heath. He not only suggested alterations—most of which were adopted—but he also expanded certain of the physiological sections. Further reference to these additions will be found in the text. Dr. G. P. Hector gave much assistance in the preparation of the chapter on "Rice"; he also read and modified the draft. In the preparation of the typescript, I am indebted not only to Miss Wyers, but to Mrs. D. E. Place and to my wife, Mrs. J. M. Hector. I have further to express my indebtedness to Mrs. J. W. Rowland in the preparation of certain of the illustrations; and to Miss S. N. Schoeman for assistance in checking literature and in many other matters.

In the reading of the proofs, I am indebted to Mr. J. B. Wyers for much assistance. The index was jointly compiled by myself, Miss S. N. Schoeman, Miss B. Stiemens, Miss E. de Villiers and Mrs. G. Kays.

Most of the illustrations have been copied from the original publications and I have to express my indebtedness to the authors and their publishers for permission to reproduce the diagrams and plates in question.

In particular, I have to mention Professor John Percival for permission to reproduce from his monograph on wheat, Figs. 24, 25, 29, 33-37, 40-42, 47; and Miss A. G. Erith, Figs. 321-327; also to the McGraw-Hill Book Co. Inc.; the Cambridge University Press (to whom I am also indebted for the loan of the blocks); the Chicago University Press; Messrs. P. Blakiston's Son and Co.; Messrs. Adam and Charles Black; Messrs. John Wiley and Co.; Messrs. McMillan and Co., and Messrs. A. and I. Churchill for the reproduction of the figures specified in the respective legends. In addition, the Editor and Publishers of the following journals:—

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205, 210-213, 244-246, 275-277, 290-300, 302-304, 306, 307, 330, 331, 333, 353, 354, 356, 360, 361, 374, 376, 381-385, 400, 412-415, 417-425, 428-430, 434, 439); *Bulletins, U.S.A. Department of Agriculture* (Figs. 87, 89, 90, 91, 138, 140-142, 279-282, 284-288, 290, 301, 313-315, 318, 334-337, 340); *Canadian Journal of Research* (Figs. 7, 10-12, 317); *Memoirs and Bulletins, Cornell University* (Figs. 79, 80, 84, 86, 162, 184); *Cytologia* (Figs. 52, 53, 68, 105, 177, 178); *Genetica* (Figs. 401-403); *Genetics* (Figs. 180, 181, 274); *Hilgardia and Bulletins of the University of California* (Figs. 201, 206-209, 151, 196, 227, 305, 399); *Indian Journal of Agricultural Science* (Figs. 99, 104, 106-108, 111, 112, 115, 116, 139, 272); *Japanese Journal of Botany* (Figs. 20-23, 297, 298); *Journal of Agricultural Research* (Figs. 17, 43-46, 48, 51, 54, 55, 57, 66, 67, 71, 82, 83, 94-96, 117-119, 122-132, 134, 135, 143, 156, 157, 159-161, 164-166, 170, 174-176, 218-226, 228-238, 240-242, 243, 247, 248, 259, 309, 310, 319, 320, 341-346, 355, 377-380, 387-397, 406-409); *Journal of Agriculture* (Fig. 308); *Journal of Genetics* (Figs. 6, 19, 56, 61-63, 260, 367-369); *Journal of Heredity* (Figs. 60, 81, 186-189, 190); *Memoirs of the Department of Agriculture, India* (Figs. 93, 98, 100-102, 113, 114, 120, 121, 133); *Proceedings of the Academy of Sciences, Washington* (Figs. 88, 182, 183); *Proceedings of the Royal Society, London* (Figs. 264, 165, 269); *Publications of the Imperial Agricultural Bureau, Aberystwyth* (Figs. 311, 312, 328, 329); *Publications of the Carnegie Institute, Washington* (Figs. 151, 196, 227, 305, 399); *Journal and Annual Reports of the Empire Cotton Growing Corporation* (Figs. 338, 339, 351, 352, 357-359, 362, 365); *University of Iowa, Bulletins* (Figs. 426, 427, 431-433); *University of Washington, Research Studies* (Figs. 58, 59, 64, 69, 70).

The author of each illustration is indicated on the legend. In the reproduction of these illustrations, I have also to thank Professor Matthews of the University of Aberdeen for the facilities given me in his department.

I am also under obligation to the Librarian, Mr. P. C. Coetzee and the staff of the Library of the University of Pretoria; to the Librarian and the staff of the Library of the Department of Agriculture, Government of the Union of South Africa; to Miss Gunn, Librarian, Division of Plant Industry; to Dr. Simpson and the staff of the Library of the University of Aberdeen; and to the Librarian, School of Agriculture, Cambridge. I have further to acknowledge my indebtedness to Dr. Hudson and the staff of the Imperial Bureau of Plant Genetics, and would at the same time pay tribute to the value and efficiency of the service of the Bureau, especially to the worker overseas.

Finally, I have to thank my friend and colleague, Professor H. D. Leppan, the Editor of this series, for his patience, encouragement and criticism (sometimes drastic, always kindly and thoroughly deserved); and also to my publishers for their kindness, assistance and forbearance.

J. M. HECTOR.

PRETORIA.

June, 1936.





## CHAPTER I

### INTRODUCTORY

THE plants dealt with in this text constitute a miscellany. They in no way form a natural system, but are distributed throughout the families of the flowering plants almost haphazardly. Partial exceptions no doubt occur. Thus the family of the Gramineæ includes practically all the "grain" crops, and some of the most important are confined to a sub-section of the tribe Hordineæ: in addition, a very large number of the non-cereal grasses have marked economic importance. Species with "lint" are also numerous in the group of the Malvales, though only two—the cottons and Kapok—have been exploited commercially. Such groupings, however, are exceptional.

As a consequence, the botanical study of crop plants tends of necessity to be too specific to be applied comparatively and phylogenetically. The data as such, however, may be of fundamental value when correlated with wider studies. Unfortunately there has been a tendency to lose sight of this data, perhaps in part due to the fact that it is markedly specific.

The study of cultivated plants has but one object—to gain a comprehensive understanding of the nature and life processes of these plants. This objective has a two-fold justification, one immediate and one ultimate. The immediate justification lies in the application of this knowledge to agriculture in the wide sense. In other words, it is economic. These economic values, however, fluctuate, and markedly so at the present day. In a world so inverted that food products are destroyed or deliberately restricted to preserve a so-called "market," it would at first sight appear that no one could be more redundant or more fatuous than the botanist or the agronomist devoting his energies to the creation of methods for increased production. Nevertheless there remains the second and ultimate justification—the human value and needs which are permanent and still far from satisfied.

To obtain a full understanding of any of the field crops, the approach must be made from every angle; from the viewpoint not only of morphology but also from those of physiology, cytogenetics, ecology and systematics. Only by so doing can we reconstruct the particular as "what it is," a living creative organism. The outlining of such a synthetic picture—always impressionistic and never precisely in focus—must be our aim.

The student should first be familiar with the form and structure of the flowering plant, and be able to apply this knowledge to the specific field plant. The more he can, as it were, "see through" a plant, the better will he understand its life processes. Structure and function are not different in kind: they are abstractions in the main due to our mode of approach. As Woodger has attempted to formulate it "The concrete organism is a spatio-temporal structure and . . . this spatio-temporal structure is the activity itself."

The physiological viewpoint cannot, therefore, be divorced from the morphological though it may be so separated in practice. Much of the data in plant physiology has been obtained by the use of crop plants. Most of these experiments, however, were carried out with such plants as the sunflower, beans, the potato, etc., not to obtain a better understanding of these plants as such but to obtain a knowledge of fundamental processes. This knowledge of fundamental processes the student, concurrently with his specific studies, must gradually build up. He will then be in a position to grasp the importance of the more direct attack that is now taking place—the attempt by physiological analysis to understand the behaviour and the reactions of particular plants in the field. This method is partly illustrated throughout the text. It is perhaps demonstrated most clearly by the work done in recent years on the cotton plant, though less unified examples are to be found in the case of other plants, *e.g.*, wheat, the potato, etc.

The ecological viewpoint connects with the physiological. Until recently, ecology played only an incidental part in agriculture. It is now, however, being increasingly realized that an understanding of the climax vegetation and the succession in any one district is the key to its agricultural potentialities. Here, in addition to a knowledge of the principles of ecology, the student should grasp the significance of the part played by climate—both the atmospheric climate and the soil climate. To attain this he should never omit in his studies a course in soil science. He should be familiar with the reaction of the plant to photoperiods and to temperature, and be able to view a “variety” as a particular “reaction system”—an “ecotype”—which must be fitted in to a “climate.” Here we are entering into what is at present a novel viewpoint—the study of “crop-ecology”—a viewpoint which is now only tentative, but which, when pursued to its logical issues, will pave the way to the development of an “adjusted agriculture,” transcending all existing boundaries and artificial barriers, local and national. This is a possibility of the future; as a probability perhaps very remote. Yet it can receive, and is already receiving, local application.

During the present century, the most striking advance in the study of crop plants has been made in the field of cyto-genetics. The plant breeder has many successes to his credit. Of greater importance is the knowledge that has been obtained of the primary endowment of plants generally and of certain of the crop plants in particular, and of the sequence of inter-related spatio-temporal actions and reactions initiated by the genes in development. The problem of the relative importance of heredity and environment—“nature and nurture”—has been largely solved, though confusion and misinterpretation may still take place. The discovery of the linear arrangement of the genes on a specifically constant number of paired homologous chromosomes has given a mathematical precision to genetic analysis, and our conceptions of “hybridity,” “mutation” and “variation” have been clarified by the application of cytology to genetics. These discoveries—together with the great wealth of new genetic material that has been obtained in Asia, Africa and South America—will yet enable the plant breeder to rebuild the “constitution” of our agricultural plants and ultimately to synthesize the existing species into new reaction systems.

In the text no attempt has been made to give detailed genetic analyses of the plants studied. Such analyses are better confined to special memoirs, and a few

have already been published (*e.g.*, Harland on *Cotton*; Eyster on *Maize*). Nevertheless, some of the facts are noted and certain of the wider principles involved illustrated and discussed. In following certain of these sections, even the senior student may find difficulty. These difficulties will but emphasize what has already been stated—that the student must, simultaneously with his study of the specific, obtain as wide a knowledge of basic principles as possible, and of cyto-genetics in particular.

The systematics of crop plants are at present in confusion. A wealth of new species and new varieties has been discovered, and most of the classifications now in use are based upon the more limited material previously available. Further, cyto-genetics and ecology have modified the whole outlook of the botanist and of the applied botanist in particular.

Whilst the newer knowledge has confirmed much of the work of the taxonomist, it has altered the status of his “species” and “varieties,” and at the same time has introduced new units of differentiation—Linneons, ecotypes, pure lines, phenotypes, genotypes and so forth. None of these concepts has yet been assimilated into any classificatory scheme. They are like new building material whose use the architect has not mastered; they are endlessly discussed but almost unutilized.

Now these units are fundamental in the classification of crop plants. For the existing unit of the Agronomist is the “variety” of the farmer—a phenotype of variable but on the whole constant expression. This so-called “variety” has a status totally different to the “variety” of the systematist. In many respects it is equivalent to the “ecotype” and its precise status for each crop species must be defined and its relation to the “species” orientated. It is basic problems of this nature that the investigator of the future must equip himself to solve.

In addition, the writer is of the opinion that the classification of crop plants has been rendered unnecessarily cumbersome by too slavish an adherence to the nomenclature of systematic botany. To extend the accepted terminology so as to incorporate in its meshes the “variety” of the agriculturist is a pedantry which produces nothing but an ineluctable obscurity. The farmer knows what a “Square-head Master” wheat or a “Chevalier” barley *is*: none but a few specialists can attach any importance to a designation such as “*Triticum aestivum* L sub-species *vulgare* (Vill) Thel. var. *turgidum* (L) Druce,” and even they may not be in agreement. When the primary “species grouping” has been accepted by common agreement, and the status of the ultimate unit de-limited, some form of numerical designation—each digit of the series having an agreed meaning and precise alternative (or alternatives)—seems inevitable for the classification of the crop plants.

In the meantime, the text gives the main species groupings now accepted, and refers the student to the more important “varietal” classifications that have been published. All these so-called classifications should be regarded as “classificatory guides.”

In the field of “origins,” the student should be content to confine himself to “immediate,” not “ultimate” origins. This limitation yet leaves a comprehensive and complex field to explore. In the study of the geographical distribution of crop plants, the de-limitation of “centres of diversity” and the correlation of

these and other facts with the data of history, anthropology and archæology, the future student of origins will find scope for all his gifts of reasoning and imagination and the exercise of suspended judgment. The full "story of a loaf of bread" is wellnigh the history of the human race.

Finally—and here the writer must ask forgiveness for the introduction of what may seem extrinsic and purely personal opinions—the student would be well advised not to neglect the study of theoretical biology in the wide sense, and also to obtain some metaphysical foundation for his scientific outlook.

Until recently the biological student, especially the student of applied biology, tended to regard theoretical biology as purely speculative and accepted a belief—almost a "faith"—in science which had little or no basis in reason. Such an attitude of mind cannot see the wood for the trees; it produces in operation only a multiplicity of facts without system or order. As a consequence, biology has but few laws and fewer theories of wide applicability. Fact and theory tend to be confused, and experimentation vague without the guidance of genuine working hypotheses. From the wider standpoint also the student must realize that "no science can be more secure than the unconscious metaphysics which tacitly it presupposes." We have recently been reminded that "naïve and stupid people are the true scientists, who make science what it is and give it practical value." In a measure and from the "practical" viewpoint, this may be true. From the viewpoint of the worth of the individual and the intellectual value of his science it is, if true, a calamity. Our stupidity may be unavoidable; our *naïveté* is a fault that can and should be rectified. There is no mental discipline to equal the critical examination of our tacit assumptions.

## CHAPTER II

### THE GRAMINEAE

THE Gramineae are economically by far the most important of the families of flowering plants. All the so-called "cereals"—oats, wheat, barley, rye, maize, rice, sorghum, millets and certain minor forms of restricted cultivation—are grasses. In certain of the eastern countries bamboos are utilized in wellnigh every phase of life. Several of the grasses are the source of aromatic oils. The annual value of the sugar from sugar-cane is in the neighbourhood of £200,000,000. Finally, it would be almost impossible to estimate the monetary value of the hay and pasture grasses, and the many million acres of natural grassland that cover large tracts of the earth. Very literally "all flesh is grass."

Most annual grasses, the cereals, a majority of the perennial grasses of the tropics and semi-tropics and many of the temperate grasses have the "bunch" or "tussock" habit variously developed. This growth form is due to the fact that only the basal buds of the main axis develop, thus producing a central axis or culm with a few basal branch culms or tillers. These tillers may repeat the process and in this manner, the bunch or tussock habit of growth is built up. On the other hand, many grasses—especially certain of the temperate grasses—have a spreading or creeping habit. In these grasses the basal buds produce elongated underground rhizomes which give rise to erect annual stems. It is such grasses, often in combination with smaller erect grasses, that produce the compact "sod" of the more temperate pastures. In the bamboos, also, a very complex rhizome-plexus is ultimately produced.

The erect or creeping habit, however, is only a matter of degree, and in the perennial grasses, all the basal buds produce branches which in some measure are rhizomatous.

In the different habitats where grasses occur these two extremes find varied expression. Two main trends of distribution may be distinguished with a third forming an intermediate series. The first of these groupings consists of the grasses of the tropical forest margins closely associated with the tropical and semi-tropical hygrophilous types. Here the typical grasses are the most primitive, and in all probability have had "the longest uninterrupted evolutionary history." They include the woody bamboos, the largest species of which may have culms a foot in diameter and over 100 feet high, although a few of the bamboos are herbaceous, and some are climbers. Some grow in dense clumps, the many culms developing from short, more or less vertical or slightly oblique, rhizomes; others are more widely spaced with the rhizomes more horizontal and more widely spread, producing culms as a consequence at greater distances. Associated with these there are many herbaceous grasses with the culms scrambling or climbing, their decumbent bases producing adventitious roots. Surrounding the tropical forests, a varying belt of very tall coarse grasses, either annual or perennial, occurs. These grasses constitute the tropical High Grass Savanna, often associated with

tree growth, regularly ravaged by fire during the dry season, and in the main dominated by tall species of the *Andropogoneae* and *Paniceae*.

High Grass Savanna is succeeded by Low Bunch Grass Savanna, covering much larger areas of decreasing rainfall and extending into the sub-tropics. It may or may not be associated with tree growth. In composition these natural grasslands differ but little from the true Savanna. The climax stages are again dominated by the tufted species of *Andropogoneae*, but there is more admixture: in the earlier stages, specialized types of the *Pooideae* are prominent, related to the climax types of the semi-desert and desert regions, into which the low bunch grass almost imperceptibly passes.

In tropical mountain areas, another transition is to be seen. The tropical sub-tropical grasses ascend to considerable heights, but ultimately merge into areas of primitive temperate grasses, at first scattered but later becoming dominant.

The second trend is to be found in temperate areas, and more or less parallels the sequence from moister to drier areas found in the tropics.

It commences with the marginal grasses of the deciduous woodlands, dominated by members of the *Festuceae* and certain *Agrostideae* and connected ecologically with the hydrophyllous and stream-bank grasses. These associations pass into the typical temperate meadows and pastures where the grasses are often tufted but inter-mixed with rhizomatous types to form a continuous "sod" consisting of a large number of species. Here many of the most valuable grazing and hay grasses are to be found naturally.

These mesophytic areas grade into drier and much more extensive areas of stable grassland which corresponds in many respects to the low bunch grasslands of sub-tropical countries. They include the tall grass prairies of the Mississippi valley, the bunch grasslands of the Western States, and the short grass grassland of the plains, situated between the tall grass prairie and the Rocky Mountains. Each of these great areas is again divisible into several sub-types. There is a transition throughout from moister conditions to semi-desert conditions. In Russia, a similar series of grasslands occur, the transition from meadow types associated with forest to semi-steppe, grass steppe and semi-desert types being again evident. Although the species are very different, the parallelism is clear.

Between the temperate and tropical areas in regions of predominantly winter-rainfall, a climax, characterized by evergreen sclerophyllous scrub, is to be found in the Mediterranean region (*Maquis* or *Macchia*), in the South-West of South Africa (*Fynbosch*) in South and South-West Australia, in California (*chaparral*) and in Chile. The grasses are numerous in relation to genera and species, but they tend to be scattered and only rarely form "grassland." They include many endemic forms, and also a large number of species of the *Aveneae*. Most are somewhat highly specialized, tufted or somewhat creeping in habit but never sod-forming, deep-rooted and hard, sometimes with almost woody basal culms. Many are annuals.

In temperate countries, both in the North and the South, minor groupings also occur. On sandy soils and along the sea coast, a number of specialized and often markedly rhizomatous types develop.

The centres of diversity of the various cereal types are discussed in relation to each species in the text.

**ROOTS.**—Grass roots are of two types, seminal and adventitious. True seminal roots are pre-formed in the embryo. Their number varies with the species and to a certain extent the variety. In annual grasses they function throughout the life of the plant and in exceptional circumstances may be the only roots to function. In the case of perennial grasses they probably cease to function after the first season.

The adventitious roots may arise from any node above the insertion of the coleoptile but are almost invariably confined to the basal nodes at or near ground level. At any one node the number varies, but usually they form a definite whorl. Each adventitious root arises endogenously, and is closely connected with the nodal plexus.

In annual grasses, the adventitious roots tend to grow out at first somewhat horizontally and then turn abruptly downwards, the depth reached varying with the species and the soil. Each whorl of roots tends to have a wider spread than the preceding one.

In perennial grasses, the functional adventitious roots arise mainly (or wholly) from the tillers and the first formed adventitious roots apparently cease to function towards the end of the first growing season. In a perennial grass, however, it is not known how long a particular whorl of roots may function.

Dimorphism has been noted in the roots of certain cereals. Thus in barley, the roots are at first thick, white and unbranched, with numerous root hairs along the entire surface. Thereafter they lengthen, become thinner and more fibrous, branch and carry root hairs only towards the apices. In the reed (*Phr. communis* Trin.), and in Townsend's Grass (*Spartina Townsendi*, H. et J. Groves), a similar but even more distinct dimorphism occurs.

The anatomy—very diversified and insufficiently studied—is partially illustrated in certain of the cereals in the main text.

**STEMS.**—In a young grass or cereal, there is at first a single main axis or culm divided into a series of inter-nodes by the nodes. This shoot is at first solid throughout, but as it elongates it may become hollow by the rupture of the pith, except at the nodes which remain solid. At first the inter-nodes are very short; later each inter-node elongates, the length attained varying with its position and the species. The ultimate height so produced may vary from a few inches to 100 feet. In general the basal inter-nodes remain short; the upper tend to become progressively longer with the uppermost inter-node, ending in the inflorescence, the longest. Growth of each inter-node is always from the base. This meristematic region is often marked by a swelling—the pulvinus. The swelling, however, may be due to the axis alone or to the base of the leaf only or to both as in *Zea*. In any case the pulvini exhibit no stomata, no inter-cellular spaces and the vessels, elsewhere reticulate or pitted, have either ring or spiral thickenings. Elongation and bending may, therefore, take place without injury.

The nodes of the axis are always solid and may be marked externally by the presence of a ring of hairs or by pigment. The apparent thickening is not at the node itself but above the node at the pulvinus. Internally, the node is marked by the presence of horizontal vascular strands which inter-connect with the vertical strands to form a highly elaborate plexus.

The culm is usually round but sometimes variously flattened. One side is



frequently grooved, the position of the groove alternating at each inter-node. In origin the groove is due to the pressure of the bud at the node enclosed in the sheath on the young soft axis. The indent so made may then be retained and expanded with subsequent growth.

In most grasses the main axis only develops lateral branches from the basal buds. These branches are the tillers. The mode of tiller formation is illustrated for the wheat plant later (see page 99). In wheat and all other similar annual types, it produces a compact bunched or tufted habit. Even in wheat, however, varieties are known in which the tillers have at first a slight horizontal spread, producing in the young plant a semi-prostrate condition. In all perennials—including those described as “bunch” forms—all the older tillers are of necessity somewhat rhizomatous in the early stages of development. As a consequence, these grasses develop a sympodial rhizome, often very short, composed of the successive lower inter-nodes of the culms, the latter forming aerial branches in turn and thus adding to the basal “crown.”

In contrast to the typical “bunch” grass, whose buds generally grow up within the sheath (intra-vaginal), there are other grasses whose buds break through the sheath (extra-vaginal) or push the sheath aside, thereafter growing for variable distances more or less horizontally as true rhizomes. From these rhizomes, erect aerial culms may arise from the nodes, in relation to reduced leaves and also adventitious roots. The result is the formation of a typical creeping or spreading grass.

The typical growth of a rhizome is more or less horizontal, sometimes for very considerable distances. Such a habit produces certain of the most dangerous weeds of arable land. In a few cases the rhizomes grow downwards as in *Festuca caerulea* Desf. In other cases the horizontally growing branches occur at or above ground level, thus producing a stoloniferous type. In some grasses the branches may function either as rhizomes or stolons according to the conditions. This is seen in *Pennisetum clandestinum* Chiov, the Kikuya grass.

Rhizomes often function as storage organs. In a few, the basal inter-nodes may become much thickened as in *Arrhenatherum avenaceum* Beauv., var. *bulbosum* Lindl. Leaf bases, however, may also function as storage organs, as in *Poa bulbosa* L and *P. flabellata* Hook. All such grasses are usually termed “bulbous.”

LEAVES.—The leaves of grasses are two-ranked or distichous, and in the case of the foliage leaf divisible into two parts, the sheath and the blade (lamina).

Leaf-sheaths vary markedly, tending to overlap at the base, sometimes considerably, but elongating above. Even at maturity, however, the higher inter-nodes may be almost completely covered or even exceeded in length by the sheaths. The width of the sheath also varies, producing when narrow a so-called “open sheath” but in others overlapping at the margins so as to produce a “closed sheath.” Their inner surfaces are usually smooth and glabrous, their outer variously grooved and either glabrous to markedly hairy. Throughout their length they are traversed by numerous fibro-vascular bundles, sometimes accompanied by abundant sclerenchyma.

At the junction of sheath and blade there is often a distinct break in the tissue, more or less V-shaped in outline. At the base of this articulation, but on the

distal inner margin of the sheath, there occurs a thin membranous outgrowth, the ligule. It is said to originate from the epidermis alone (Bugnon, 1921), but in some cases it is partly or fully vascular. The relative development varies enormously in different species and it is often of diagnostic value. Absence of ligule in a cereal is usually a recessive character.

Above the ligule, lateral outgrowths known as auricles may occur, well developed in *Hordeum* and *Oryza*.

A long, narrow flat blade tapering to a point and with numerous parallel veins is typical of most grasses. In many species, however, the normal facies may undergo considerable modification. Certain of the tropical forest grasses possess a blade which is markedly broadened and often asymmetrical; in some of these the blade narrows to a distinct petiole, which may reach a length of 5 inches in *Panicum sagittaeifolium* Hochst. Certain of the more xerophytic species, on the other hand, have almost solid leaves, deeply grooved or furrowed as in species of *Sporobolus*, *Aristida* and *Deschampsia*.

Anatomically the grass leaf shows many characteristic features. Thus the cells of the epidermis are often so characteristic in their shape, relative position and development (e.g., the "motor" or "bulbiform" cells) that they may be used for the differentiation of species and even varieties (see *Saccharum*, pages 329-331).

The fibro-vascular bundles in many have two sheaths, the outer parenchymatous and with or without chlorophyll, the inner resembling in appearance an endodermis. In *Zea Mays* and other species the inner sheath is absent, the parenchyma sheath itself becoming somewhat thick-walled. The bundles themselves vary too in number and size and in the amount and position of associated sclerenchyma. The chlorophyll containing tissue also exhibits variability, one group of grasses having the chlorophyll only in the cells round the bundles, another group having the chlorophyll uniformly distributed.

The lateral buds of the grass are enclosed in a bi-keeled first leaf—the prophyll—which resembles in some respects the coleoptile. It faces the axillant leaf and, to use Arber's term, is "addorsed" to the main axis. It has been interpreted both as a single leaf and as a fusion of two leaves. (See under Maize, page 403.)

**INFLORESCENCE.**—The entire inflorescence of a grass bears spikelets, not single flowers. Each spikelet is a group of one or more flowers with a number of associated bracts, and as such is the unit of the inflorescence. Nevertheless it is convenient to speak of the whole branch system carrying the spikelets as "the inflorescence," in spite of the fact that in reality it is a compound system. On this basis the spikelets are carried on a type of branched raceme which in many instances can perhaps best be described as a panicle. In such a system, the main axis carries a number of lateral branches whose basal inter-nodes are so abbreviated that the lateral branch itself and one or more of its secondary branches, precociously developed, appear to form a pseudo-whorl at the nodes. This appears to be the most primitive form. In the oat plant (see page 23), this mixed form is well illustrated. Sometimes the panicles may become one-sided, as seen in certain varieties of oat, or partially so, as in *Dactylis glomerata* L., where the symmetry is more dorsiventral than radial.

All other forms of the grass inflorescence may be derived from the paniculate type by a process of simplification due to contraction, condensation and reduction.

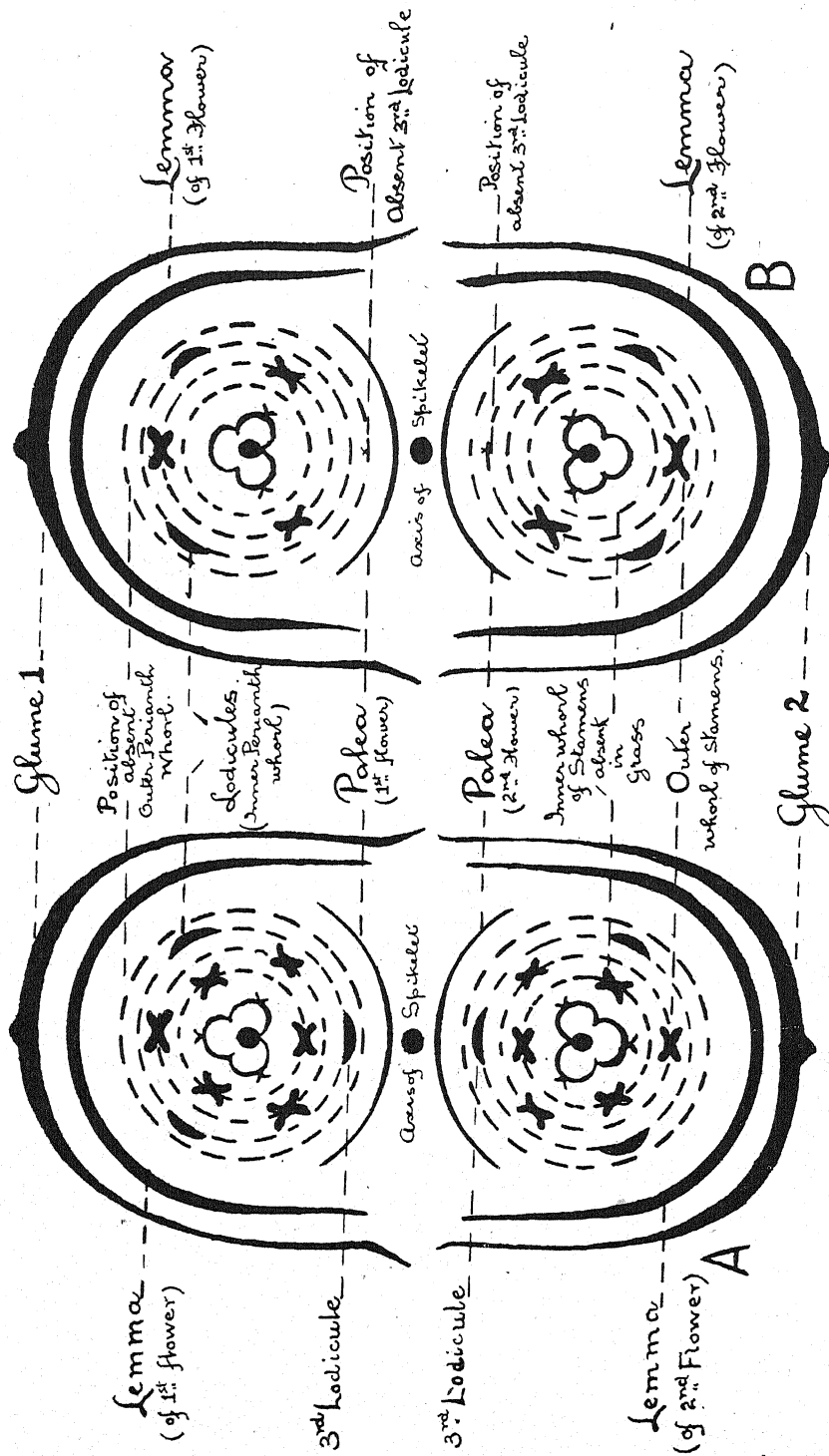


FIG. 1. Schematic interpretation of the Grass Spikelet.

- A. The Bamboo Type (3 Lodicules ; 2 whorls of Stamens ; 3 carpels each with styles).  
 B. The Grass Type (2 Lodicules ; 1 whorl of Stamens (inner absent) ; 3 carpels with two styles (front style absent)).

The first stage is seen in the production of a contracted panicle which is spike-like in appearance. In the cereals, this is illustrated by the contracted panicle of many of the Sorghums and in the more spikelet inflorescences of *Setaria italica* and *Pennisetum*.

The second is to be seen in many of the Chlorideae. By contraction and reduction a sparingly branched system forms in which each branch is racemous, the spikelets frequently arranged on one side only of the branch axis. In such forms, the few branches produced may arise in a racemous manner along the main axis, or be situated at or near the apex of this axis. The racemes are then digitate or sub-digitate in position (e.g., *Eleusine coracana*). Rarely the raceme may be solitary as in species of *Harpechloa*.

The third stage is one in which the spikelets become sessile on the main axis, thus producing a spike of spikelets. This arrangement is well seen in all the Hordeae, and is exemplified in the cereals by barley, rye and wheat. Often the spikelets are somewhat sunken in the axis (rachis) and so afforded increased protection. This result, however, is due in the first instance to mechanical pressure. The swelling spikelets on the soft growing axis are compressed within the leaf bases and as a consequence the rachis is moulded against the alternately arranged spikelets.

**THE SPIKELET.**—A spikelet consists of one or more flowers in association with a number of bracts. The spikelet may be borne on a stalk or pedicel, which may be elongated, short or absent. When present the pedicel is continuous with and is a modification of the lateral axis carrying the spikelet.

The most generalized form of a spikelet has the following structure :—

There is first a short axis or rachilla whose length depends mainly on the number of flowers it carries. At the base of this axis, there are two sterile bracts, the outer and inner glume or first and second glume. The outer in part envelops the inner, their insertion being very close but at opposite levels. Above the glumes there are one to several flowers (florets), arranged in a distinctive manner, the first (or only) inserted at a nodal point immediately above the outer glume; subsequent flowers are, if present, situated similarly in regular succession. Each flower is in turn subtended by a bract, the lemma (flowering glume or valve), i.e., the flower is situated in the axil of the lemma. Opposite the lemma a second bract occurs—the palea (pale, palet, valvule or bracteole)—situated at the base of the very short floral axis on the posterior side of the flower between it and the rachilla. Lemma and palea normally enclose and protect the flower proper. (Fig. 1.)

Analysing the flower proper, three structures are represented.

(1) The lodicules—which may be regarded as representing the *inner* perianth members. They are small, greenish, scale-like structures and are usually two in number, but in a few grasses and most bamboos there are three.

(2) The stamens—usually limited to the three members of the outer whorl: in bamboos and in rice, however, the inner whorl is also represented.

(3) The Gynaeceum, which is best regarded as a fusion of three carpels. The relative position of the parts is illustrated in Figs. 1 and 2.

This generalized spikelet form is subject to very varied expression.

The most important evolutionary trend has consisted in a reduction of

flowers in the spikelet. This reduction is generally from above downwards. Two flowered spikelets are common. The upper flower may then become staminate or aborted with the lemma and palea or lemma only present on the rachilla tip. (Fig. 3 (a).) In some cases only the rachilla tip is left. Finally the spikelet may become strictly 1-flowered and purely terminal.

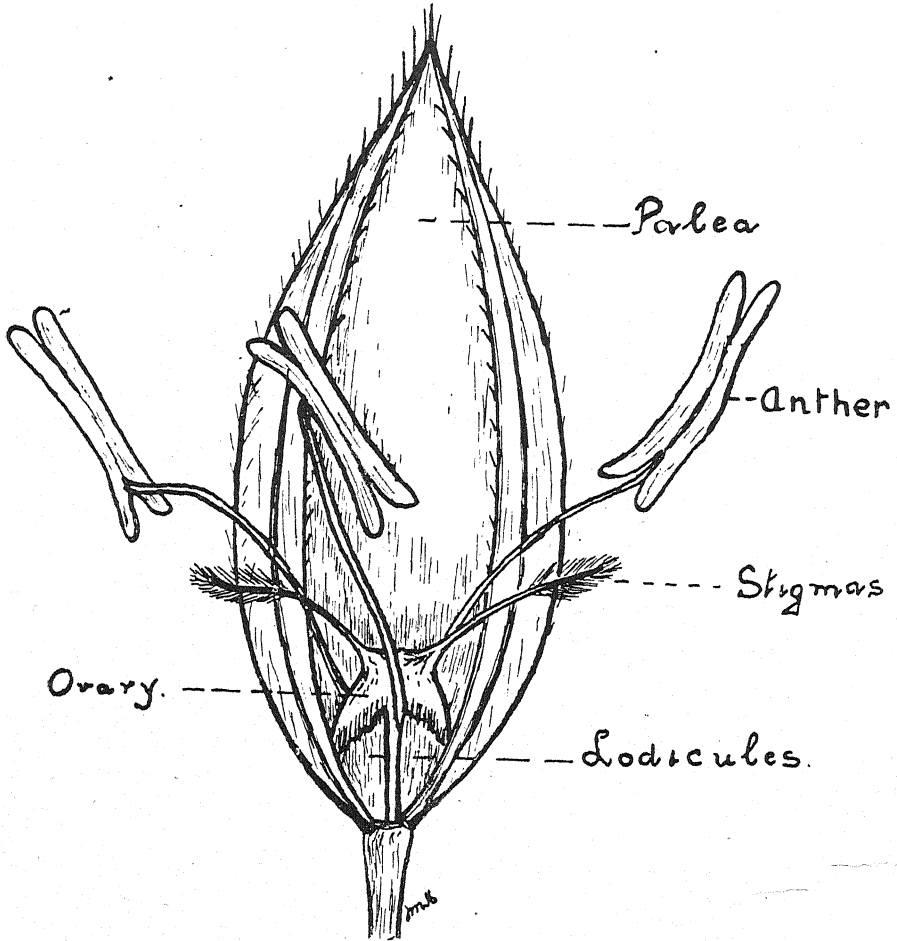


FIG. 2. Diagram of Grass Flower with Lemma removed.

Reduction, however, may occur in the lower flowers. (Fig. 3 (c).) Thus the first flower may become staminate or abort, being represented by its lemma or palea or lemma only (pistillate spikelet of maize, sessile spikelet of Sorghum, etc.).

In some instances, a spikelet may become staminate or pistillate only.

Variation in size, shape and texture, etc., of the various parts is frequent.

The rachilla varies in size mainly in relation to the number of flowers. The glumes may be large and more or less equal in size as in *Avena*; sub-equal or markedly unequal. They may be larger than the lemmas or markedly smaller.

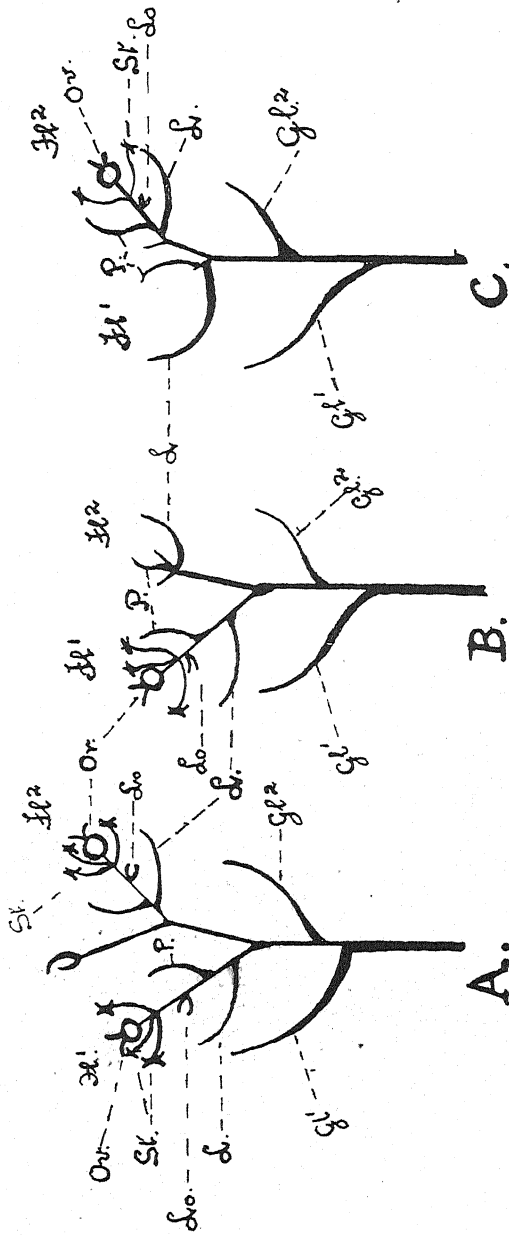


FIG. 3. Schematic Diagram of Spikelet Types.

- A. Spikelet with two fertile flowers and rudiment of third.  
 B. Spikelet with first flower fertile and second infertile: reduction from above downwards.  
 C. Spikelet with first flower infertile and second flower fertile: reduction from below upwards.
- fl<sup>1</sup>, first glume; gl<sup>2</sup>, second glume; fl<sup>1</sup>, first flower; fl<sup>2</sup>, second flower; l, lemma; P, palea; lo, lodicules; st, stamens; ov, ovary.

Shape and venation are often markedly characteristic. The apex may be bifid at times or prolonged into an awn.

Equal variability is found in the lemma which usually bears the "awn" when present. Generally the awn is a prolongation of the apex and is unbranched. Branched awns, however, are known in many species. An awn may also arise in the sinus between a lobed lemma or spring from its back as in *Avena*.

The palea is subject to less modification in expression. It is usually two-nerved or two-keeled, somewhat flattened, with its margins enfolded around the flower. Often, however, it suffers reduction, and is frequently obsolete.

**SEX-EXPRESSION AND POLLINATION.**—Dioecism—when the staminate and pistillate spikelets occur on different individual plants—occurs sporadically, e.g., in *Buchloë dactyloides*, Engelm.; *Eragrostis reptans* (Michx.) Nees, *Jouvea pilosa* (Presl.) Soubn. Monoecism—staminate and pistillate spikelets on the same individual plant—is found in species of the *Maydeae*, including *Zea*, and in certain other groups. Polygamy—the presence of bisexual and unisexual (usually staminate) flowers on the same spikelet—is somewhat common, especially in the Andropogoneae.

The commencement of flowering is usually marked by a lateral spreading of the inflorescence in all paniculate types, often due to the swelling of pulvini at the base of the laterals or sub-laterals. In any one inflorescence, anthesis usually commences near the apex, spreading thereafter upwards and downwards.

Individual flower opening is in the main due to the lodicules which suddenly become swollen at the base and thus force the lemma outwards. Almost simultaneously the stamen filaments elongate and in a few minutes the anthers emerge between the spreading bracts. Meanwhile, the styles fall apart and the stigmatic plume spreads.

As a consequence, cross-pollination normally results, the pollen, light and smooth, being transferred mainly through the agency of the wind.

Self-pollination is also effectively prevented by the development of dioecism and monoecism. In monoecious plants and also in normal hermaphroditic plants, a further check against self-pollination may occur. Either the stamens of an individual flower mature before the stigmas become receptive—the protandrous condition—or the stigmas are receptive before the stamens shed their pollen—the protogynous condition. Protandry is the commoner, but there is always a period of over-lap. Self-sterility in varying degrees is also known.

Self-pollination, however, occurs and may indeed be more frequent than the evidence at present indicates. Thus in the cereals—studied in this respect in more detail than other grasses—it is now known that in wheat, oats and barley there is more self- than cross-pollination. This is due to the fact that some pollen is shed during the period of filament elongation. Recent studies of certain of the pasture grasses also indicates that much selfing may there take place.

Certain of the cereal types which show a marked tendency to self-pollination approach the cleistogamic condition, i.e., flower opening may be markedly reduced. True or partial cleistogamy is known in a number of species. Thus, *Triplasis purpurea* Chapm., carries solitary sessile cleistogamic flowers in addition to normal. Several species of *Danthonia* behave similarly. An extreme example of cleistogamy is found in the American species, *Amphicarpum floridanum*

Chapm., whose spikelets are borne on underground shoots, and but rarely forms aerial spikelets.

**ORGANIZATION OF OVULE AND FERTILIZATION.**—The structure of ovary and ovule is fairly uniform throughout the Gramineae and is subsequently described and illustrated for certain of the cereals. The presence of an incomplete second integument—later absorbed—and a tendency to the multiplication of the antipodal tissue should be noted.

Fertilization follows pollination within a variable but comparatively short period of time. The first male nucleus unites with the egg nucleus and the second with the two polar nuclei. Two functional cells are thus formed—the zygote, developing into the embryo and the primary endosperm “nucleus,” forming in time the endosperm. Hetero-fertilization has also been noted (see page 422).

**THE FRUIT AND SEED.**—The grass “seed” or “grain” is in reality a fruit, technically a caryopsis. In such a fruit the modified ovary wall—the pericarp—is intimately fused with the seed coat or testa and the whole forms a dry indehiscent unit.

The union of pericarp and testa, however, may be less intimate. In *Eleusine*, the seed has a well-developed testa which is enclosed by a thin pellicle, the remnant of the partially absorbed pericarp; a similar utricle type of fruit is found in the genus *Sporobolus*. Certain of the bamboos develop a berry-like fruit and others, a nut-like fruit.

At maturity the naked caryopsis may fall from the spikelet as in the species of *Eragrostis*, where the “seed” is extremely small (e.g., *Eragrostis abyssinica* L., the Teff Grass). Usually lemma and palea adhere to the caryopsis, either loosely or intimately or (as in certain barleys) in organic union. In such types, disarticulation takes place above the glumes. In other instances, the whole spikelet falls, with or without the glumes adhering. The most complex condition is found in species like *Tragus racemosus* (L.) All., where several spikelets together form a single fruit complex.

The caryopsis, as such, varies in size and shape, reaching a maximum in the cereals. Even within a single species, however, considerable variability may be encountered, particularly in *Zea Mays*.

The structure of the caryopsis of several species is discussed later. The pericarp is normally thin; the testa is so reduced that it can only be differentiated with difficulty. The main mass of the seed consists of the endosperm, a hypertrophied mass of tissue constituting the food reserve. At the base of the lower surface the embryo is situated in close contact with the endosperm.

Embryo structure is fairly constant. In contact with the endosperm and attached to the rest of the embryo near the middle of its front face, there is to be found the so-called scutellum. It is usually oval in outline, flat or convex on the inner face; flat or slightly concave on the outer. Its margins may be infolded so as to partially enwrap the embryonic axis which is continuous with the scutellum at a point very near its centre. This embryonic axis consists of the plumular bud at one end and the radicle at the other. The plumule—separated from the point of attachment of the scutellum to the axis by a short interval (sometimes almost absent) which has been termed the “mesocotyl”—consists of a protecting sheath,



the coleoptile, a variable number of rudimentary leaves and the actual growing point. The radicle is also enclosed in a thimble-like sheath, the coleorhiza, which splits away from the root initial early in the ontogeny. (See Figs. 9 and 44.)

Above the junction of root and axis, a tongue-like flap of tissue—the epiblast—is situated, almost opposite to the scutellum. In several species the epiblast is rudimentary or absent.

Very divergent views have been expressed on the homologies of these structures, and only a brief outline of the explanations advanced can here be given.

1. Scutellum and coleoptile together form the cotyledon, the interval between them being regarded as an extension of the cotyledonary node; the epiblast is either an appendage of the axis, scutellum or coleorhiza. This view has had many supporters since the commencement of the nineteenth century. It has been advanced in recent years more particularly by Sargent and Arber (1915), Worsdell (1916), Nishimura (1922), Souèges (1922), Howarth (1927) and Arber (1925 and 1934). The arguments advanced by these investigators have been many and cannot be summarized without injustice. In Arber's words "The conclusions . . . may be recapitulated as follows, with the qualification that they are all tentative. The scutellum represents the distal sucking region of the cotyledon and is equivalent to the blade of the foliage leaf, while the coleoptile is equivalent to the ligule of the foliage leaf, the basal sheath being suppressed. The mesocotyl is the cotyledonary node, elongated by intercalary growth in its upper region. The epiblast and the coleorhiza are non-vascular outgrowths which may perhaps be compared with such non-foliar excrescences as the rachilla-flap of certain Gramineae" (Arber, 1934).

2. The scutellum is the cotyledon: the coleoptile is the third leaf or first leaf of the plumule: the epiblast, when present, is a rudimentary cotyledon: the "mesocotyl" is inter-nodal. In recent years this view has been advocated—though not in similar terms—by Coulter (1915), Weatherwax (1920 and 1923) and Percival (1921).

3. The scutellum is the cotyledon: the coleoptile the second leaf, or first leaf of the plumule: the epiblast of no significance or an appendage of the axis: the "mesocotyl" is an inter-node. This view has been clearly stated by Avery (1930) and by Boyd and Avery (1936).

4. The scutellum is the cotyledon and the second leaf: the coleoptile is the third leaf (perhaps a fusion of two): the epiblast is the first leaf.

This interpretation has been advanced by McCall (1934), and is in some respects an extension of Avery's position. It differs from all others in recognizing the cross-axis procambial plate, separating the primary root and the stem, as the first node. Associated with this node is the first leaf, the epiblast and the first of the secondary seminal roots. The second node is almost immediately above and is associated with root origins and the scutellum, interpreted as the second leaf and the functional cotyledon. A short inter-node separates the second from the third node which is associated with the third leaf, the coleoptile. This interpretation, therefore, also regards the "mesocotyl" as inter-nodal.

McCall's interpretation is simple. Yet it is difficult to accept his interpretation of the epiblast as the first leaf, and the plate between root and stem as the first node.

**GERMINATION AND THE SEEDLING.**—The majority of grass seeds require a rest period before germination. The period varies with the species, and many of the cereals may germinate almost immediately. The conditions for germination—temperature, light, moisture, etc.—vary with the species, and are practically unknown except for a few of the economic types.

On germination, the coleorhiza appears first as a glistening knob at the base of the grain. Very soon it is ruptured by the primary seminal root; later the secondary seminal roots appear. The total number of seminal roots is approximately constant for each species. They spread horizontally at first and then grow more or less vertically downwards. Meantime, the coleoptile breaks through the pericarp at the opposite end. Growth of the coleoptile appears to be due to increase in size (and differentiation) of its individual cells and not to cell multiplication. In all grasses, however, the coleoptile is raised to ground-level unless planted too deeply, piercing the ground as a light green spear.

This raising of the coleoptile node is due to growth of the axis between the coleoptile node and the junction of root with stem. The interval has been termed the “mesocotyl.” It has been variously interpreted, but in the text it is treated as inter-nodal. The inter-node, however, which mainly contributes to the elongation of the basal axis appears to vary with the species. It has, however, only been studied in a limited number of species.

Once above ground level, the apex of the coleoptile splits, and the first foliage leaves pass out and unfold. About the same time the node of the first foliage leaf commences to thicken and forms the first crown node. It is usually situated not more than half an inch below ground level. Immediately above this node the first adventitious roots develop, followed by those from the nodes immediately above in regular succession.

**CHROMOSOME NUMBERS.**—Cytological studies of grass species have, until recently, dealt mainly with the economic types. A few comparative studies have, however, been published (Church on the meiotic phenomena of several families, 1929, a and b; Senjaninova-Korczagina on *Aegilops*, 1932; Peto on *Agropyron*, 1930; Avdulow, 1931, 1933, and Hunter, 1934, on the general karyology, etc.). The chromosome numbers found are frequently high, and there is marked polyploidy in certain genera (e.g., *Avena*, *Triticum*, *Hordeum*, *Aegilops* and *Agropyron* where Prat (l.c.) found almost a complete series from diploid to decaploid).

According to Avdulow (1931 and 1933), followed by Hunter (1934), three groups may be distinguished: (1) Species with chromosomes in multiples of 9 or 10, rarely fewer; (2) Species with chromosomes in multiples of 7 or less, rarely 9; (3) Species with chromosomes in multiples of 12. The third group, however, is imperfectly known.

**CLASSIFICATION.**—Although the grasses constitute a very natural group of plants, they include so many species and have evolved so many variations of the fundamental unifying facies, that it is not surprising that systematists differ considerably in the detail of their classification.

Brown (1810) first recognized two sub-families, the Panicoideae and Pooideae, differentiated mainly on the number and nature of the flowers within the spikelet. In the Pooideae, the spikelets—usually laterally compressed—are two to many

flowered, and if reduced, the reduction is from above downwards. At maturity the florets disarticulate ; if the spikelets fall entire then they do not consist of two heteromorphous florets. In the Panicoideae, the spikelets, except in the case of unisexual and neuter spikelets, have one terminal floret which is perfect and a lower floret which is either staminate or neuter. The spikelets are usually dorsally compressed and at maturity fall entire from the pedicels, singly or in groups. Until recently, later systematists have arranged their classifications within this framework, differing, however, in the number of the tribes and in the position and number of the genera recognized (Bentham and Hooker, 1883 ; Hackel, 1887 ; Stapf, 1897 and 1917 ; Hitchcock, 1920, etc. ; Bews, 1929).

Bews, however, both adapted and modified the work of his predecessors. He recognizes eleven tribes in the first sub-family and four in the second. Of the tribes in the first family, the Avenae contains the genus *Avena* ; the Chlorideae, the genus *Eleusine* ; the Hordeae, the genera *Hordeum*, *Secale* and *Triticum*, and the allied genera *Pariana*, *Agropyron*, *Haynaldia*, *Aegilops* and *Lolium* ; the Oryzeae, the genus *Oryza*. In the second sub-family (Panicoideae), the Paniceae contain the genera *Panicum*, *Setaria* and *Pennisetum* ; the Andropogoneae, the genera *Saccharum* and *Sorghum* ; and the Maydeae, *Zea* with the allied genera *Tripsacum* and *Euchlaena*. Thus the most important of the cereals are concentrated in one tribe—the Hordeae—and, following Prat, in one sub-division, the Triticeae (in which he includes *Agropyron*, *Triticum*, *Secale* and *Haynaldia*), except *Hordeum*, which he places in the second sub-division Hordinae. Much of the most detailed work on grasses that has been done, therefore, deals with only a very small section.\*

Avdulow (1931 and 1933), followed by Hunter (1934), in a karyo-systematic study of grasses, has advanced a classification which differs in many respects from the above. He recognizes two sub-families, the Sacchariferae (Harz) Avd., and the Poatae (Hitchcock) Avd., the latter sub-divided into the Festuciformes and the Phragmitiformes. The two sub-families are separated on the following basis. The Sacchariferae are limited almost entirely to the tropics and sub-tropics. They have chromosome numbers in multiples of 9 or 10, rarely more or less ; the chlorophyll is localized in two layers round the bundles ; the main bundles of the leaf alternate with several or many secondary bundles ; two-celled hairs are often present on the leaf epidermis ; the ligule usually consists of a ring of small hairs ; the first leaf is elliptical or lanceolate and grows out horizontally. On the other hand, the Poatae are mainly temperate except for the Phragmitiformes which are tropical and sub-tropical. They have chromosomes in multiples of 7 or less, rarely 9 (except in Phragmitiformes where the chromosomes are small and in multiples of 12) ; the chlorophyll is distributed throughout the leaf parenchyma ; the main bundles of the leaf alternate with one, two or at most four, secondaries ; two-celled epidermal hairs are absent ; the ligule tends to be membranous ; the first leaf is linear and grows vertically.

The student should, however, consult the originals in order to gain an adequate idea of the inter-relationships and the position of the cereal types.

\* See also, Prat, H., 1936. La systematique des Graminées. Ann. Sci. Nat.: X Ser. Bot. 18: 165-258.

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## CHAPTER III

### OAT SPECIES (AVENA)

THERE are several species of oats, all of them cultivated either as summer or winter annuals. The following description applies in particular to *Avena sativa* (= *A. fatua* s.sp. *sativa*), and *Avena Byzantina* (= *A. sterilis* s.sp. *Byzantina*), the species which include the vast majority of the cultivated varieties.

ROOTS.—1. SEMINAL ROOTS.—The primary seminal root is derived from the radicle and is the first part of the seedling to appear on germination. Later, a pair of laterals develop almost simultaneously, followed at times by a further pair. This gives a possible total of five seminal roots. The number, however, tends to vary. Thus, Smith and Walworth (1918), found that the number varied from 0 to 5 (excluding the primary seminal root) with the mean ranging from 2.0 to 2.9.

Several authors definitely state that these seminal roots function for only a limited period, "The older root system perishes by degrees; the cauline roots first (secondary seminal roots) and then the primary root." Again, however, the observations of Weaver (1926) and also those of Rostmistrov (1909) negative this general belief.

In the earlier stages, one of the seminal roots tends to grow almost vertically downwards. The remainder grow downwards at an angle varying up to 45°. All are unbranched, and beset with root hairs throughout their length.

Later, most of these roots reach a considerable but variable depth (3 to 4 feet) and are branched throughout. At maturity they are still active. A penetration up to six feet and over has been recorded (Weaver, 1926).

2.—ADVENTITIOUS ROOTS.—The adventitious roots first develop at a node near ground level, and may become very numerous. They tend at first to grow either horizontally outwards for a distance of 10 to 12 inches, or at a varying angle downwards. They soon fill the first 10 inches of soil, and appear to branch throughout their length. Later, a few show a tendency to continue the horizontal growth outwards. The majority, however, ultimately curve downwards, reaching depths varying from 1 to 5 feet. The general habit of the oat is thus to establish a well-developed superficial system penetrating the whole of the first foot of soil and extending laterally for a foot or more; and also to produce a number of more deeply penetrating roots, which may reach a depth of from 2 to 6 feet. (Fig. 4.) In the majority most of the seminal roots function throughout the life of the plant.

Weaver (1926) summarizes the average condition as follows: "A lateral spread of 6 to 11 inches, a working depth of 2 to 5 feet, and a maximum depth of 4 to 5 feet are usual."

The root system, as in other cereals, is markedly influenced by soil and water conditions.

STEM.—The oat stem has 4 to 8 inter-nodes, generally thicker and softer

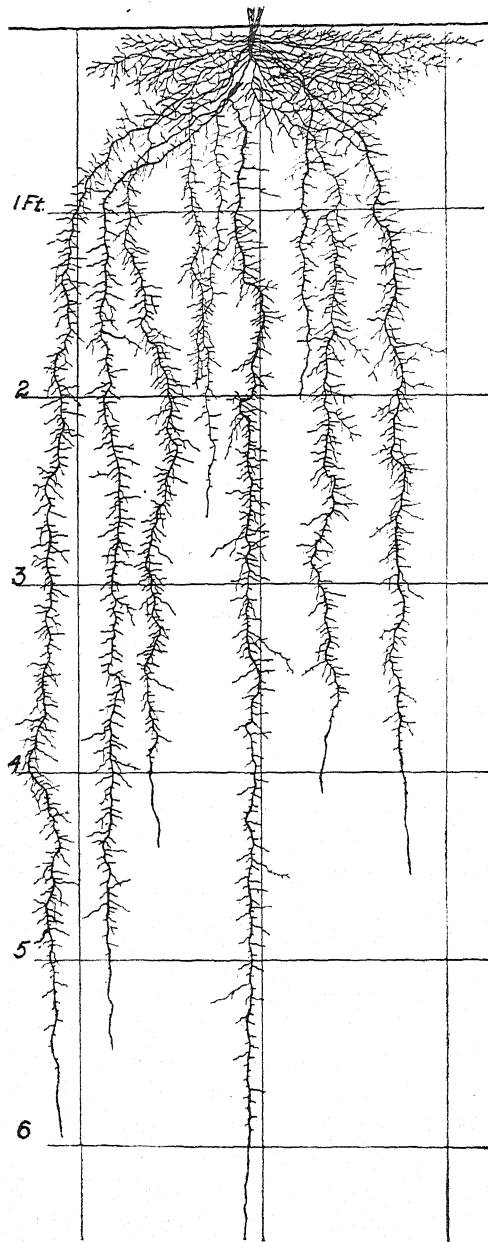


FIG. 4. Swedish select oats at maturity.

After Weaver, *Root Development of Field Crops*, by special permission of the McGraw Hill Book Co.)

than in wheat. Certain varieties are somewhat hairy (villose or pubescent), immediately above and below the nodes. The tillers develop as in wheat, but are fewer in number. Their development is markedly influenced by environmental conditions. In a few, there exists a tendency for a branch to form from the uppermost node.

In the young plant, the habit of the tillers may vary. Three main types occur—prostrate, semi-prostrate and erect. The differences may be noted even in mature plants but the distinction between semi-prostrate and erect forms is then somewhat difficult.

As in wheat, lodging of the oat is a common phenomenon. Some varieties as in wheat appear to be better anchored; in others, there appears to be a positive co-relation between non-lodging and thickness of sclerenchymatous cell walls. (Garber and Olson, 1919.) Environmental conditions play a decisive rôle. Welton and Morris (1931), conclude that "on rich ground, the chain of sequence appears to be hyper-nutrition, low carbohydrate-nitrogen relation, a preponderance of vegetative growth and straw weakness. On poor soils the reverse is true: a high carbohydrate-nitrogen relation, a reduction in proportion of vegetative growth and straw strength." (See Wheat, pages 101-103.)

LEAVES.—The leaf sheath closely envelops the axis, but is united at the base. It generally varies in colour with the blade and is in some varieties pubescent.

The ligule (absent in certain varieties, especially in *A. sativa orientalis* (= varieties of *A. fatua* s.sp.)) is well developed, oval in shape, and ends in a number of fine teeth. There are no auricles. At the junction of sheath and blade, there is a break in the tissue—the so-called "collar," which Etheridge (1916) terms the "auricle." In most oats this collar is well developed, but in certain varieties it is absent, the leaf being approximately continuous in structure with the sheath and with no ligule developed. The leaf blade varies considerably. The colour ranges from a dark glaucous green to a light. The habit may be drooping or erect. In some the blades are long and narrow, tapering to an acute apex; in others, they are shorter and broader, narrowing somewhat suddenly at the apex. Fine hairs are often present on the back and on the margins, and this character (especially when studied on younger plants) is so constant that it may be used to differentiate certain varieties.

INFLORESCENCE.—The inflorescence in the oat is a panicle of spikelets. The main axis or rachis is either erect or pendulous and terminates in a spikelet. It possesses 4 to 9 nodes, the average number being 5 to 6. At each node, a main lateral branch develops, these branches being arranged alternately, the system as a whole being racemose.

Each main lateral is again branched, the lowest being the most profusely branched. The others carry fewer and fewer branches as you pass upwards, the topmost lateral being generally unbranched. The system of branching, however, on the laterals is not racemose but cymose. In many cases it is difficult to interpret. There is a general tendency throughout for all the lower branches to be so crowded together, that certain of the lower nodes of the main axis may appear to be carrying not one main lateral branch but a whorl of laterals of varying size. (Fig. 5.)

Each lateral branch ends in a slender pedicel terminated by a spikelet. In certain varieties of *A. fatua* s.sp. *sativa* (= *A. sativa orientalis*) and others, the panicle is one-sided or unilateral, due to the fact that the lateral branches all converge to one side. There is here also a tendency for the first whorl of laterals to develop above the true node, thus producing a false node situated an inch or more above the true point of origin.



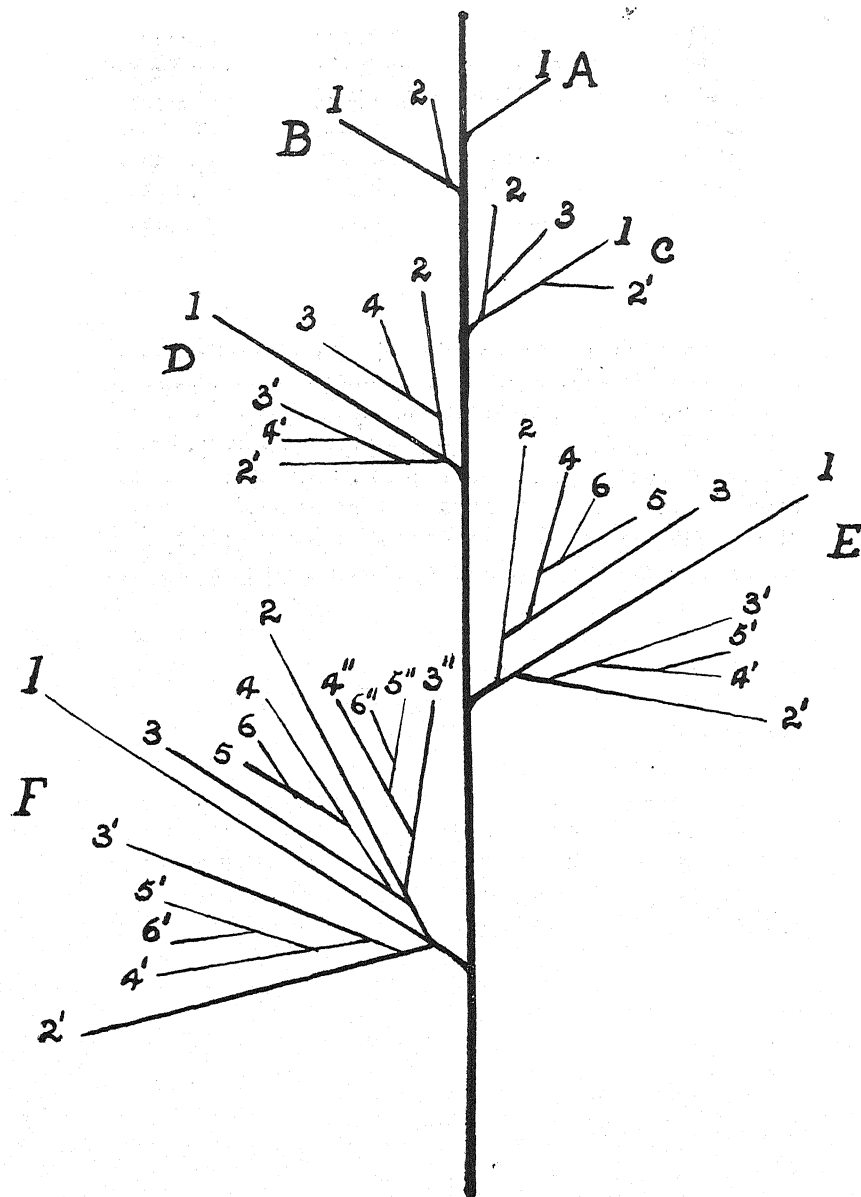


FIG. 5. Diagram of Inflorescence of the Oat. (After Broili.)

The habit of the panicle as a whole may be erect or pendulous; somewhat variable intermediate conditions of these extremes are frequent. In most varieties, the spikelets are pendant; in many of the sativa forms they are pectinate (arranged in one plane) or confused (pointing in several directions).

**SPIKELETS.**—The oat spikelet consists of from 1 to 7 flowers (florets) enclosed in a pair of bracts—the glumes. The average number of florets is three. One (the basal) or two and occasionally three of these florets may mature. Generally the upper florets are either staminate or imperfect.

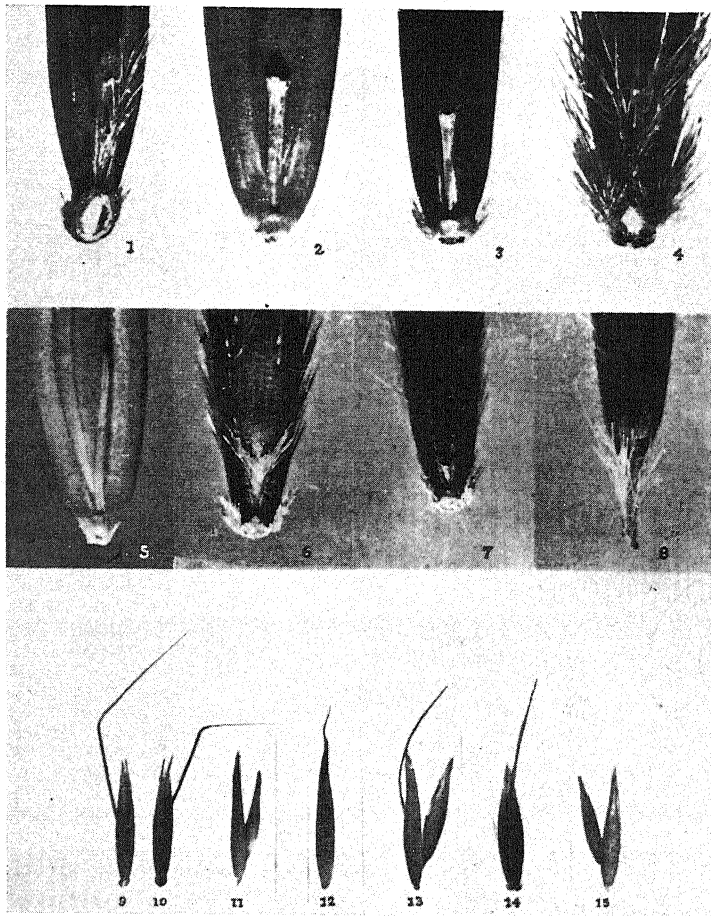


FIG. 6. Variation in articulation of Oat species.

1. Ventral view of lower grain of *A. fatua*, showing basal "sucker" and short pubescence.
  2. Ventral view of lower grain of *A. sativa* var. Banner, showing absence of "sucker" and glabrous base and rachilla.
  3. Ventral view of lower grain of *fatua* x *sativa* F<sub>1</sub>, showing intermediate condition of base, pubescence on lateral sides of base and glabrous rachilla.
  4. Ventral view of wild type F<sub>2</sub> plant with long pubescence on base and on rachilla.
  5. Ventral view of upper grain of *A. sativa* var. Banner, showing absence of "sucker."
  6. Ventral view of lower grain and dorsal view of upper grain of an F<sub>2</sub> plant, showing intermediate base with rather long pubescence on the rachilla of lower grain.
  7. Ventral view of lower grain of No. 6 showing basal fracture of the rachilla (as in *A. sterilis*).
  8. Dorsal view of upper grain of No. 6 showing pubescence and attachment of the rachilla of the lower grain.
  - 9 and 10. Ventral and dorsal view of lower grain of *A. fatua*, showing pubescence, articulation and geniculate awn.
  - 11 and 12. Side view of spikelet and dorsal view of lower grain of *A. sativa gigantea*.
  13. Side view of *A. sativa* var. Banner, showing a slightly twisted awn on the lower grain.
  14. Dorsal view of lower grain of *gigantica* x *fatua* F<sub>1</sub>, showing medium long pubescence and a weak straight awn.
  15. Side view of spikelet of *fatua* x *gigantica* F<sub>1</sub>, showing pubescence.
- (After Philp.)

The two glumes are generally equal in length; more rarely they are sub-equal or markedly unequal, and are inserted close to one another. The outer or lower practically enfolds the upper and in the early stages of development the two together form a complete protection to the enclosed florets. Each glume is thin and membranous, lanceolate, acute, glabrous and more or less boat-shaped, with from 7 to 13 (average 9) well-defined veins.

The flowers (florets) are arranged alternately and are sessile on a short rachilla. The attachment of each to the rachilla is variable and is discussed in detail below.

The outer or lower bract is the lemma. It is more or less ovate-lanceolate in outline and broadly convex; membranous to coriaceous in texture; glabrous to hairy, especially on the back and towards the base. The apex is either slightly toothed or divided (bidentate or bisulcate), or in certain sections extended into two awn-like points (biaristulate). The number of veins varies from 5 to 10, with an average of 7 in cultivated forms.

At the base of the lemma, well seen in the mature grain, a swollen calosity is present known as the callus. This callus may carry more or less conspicuous bristles, generally termed the basal hairs. They may be long or short and few to many. (Figs. 6 and 7.) The shape of the callus varies, and in many—especially the non-cultivated forms—it carries a cavity—the cicatrix, scar or “sucker-mouth,” which varies markedly in size and shape. (Figs. 6 (1) and 7, A.)

When an awn is present in the oat, it springs from approximately the back of the lemma, and is an extension of the mid-rib. In wild forms, it is found in all grains of the spikelet and is strongly developed, geniculate and twisted below the knee. (Figs. 6 (9 and 10) and 7, A.) A few cultivated varieties also have awns fairly well developed and occasionally geniculate. In the majority, however, the awn if present is found on the lower grain only and is usually small, curved or straight and untwisted. (Fig. 7, C.)

In the cultivated types, the expression of the awn may vary. Further, strongly awned forms may appear suddenly. Most of these types are now known to be of the nature of “fatuoids,” exhibiting not only the strong awn but certain other correlated characters (see page 31 and pages 61-71).

Kovalevsky (1932) studied the awn “type” and the percentage of awned spikelets of a large number of oat species and varieties at various stations in the U.S.S.R. He found that the typical expression varied from strongly awned to awnless. Although certain of the intermediate types showed considerable variation the environment only accentuated or decreased the expression of the inherent characteristic. Thus the percentage of awned spikelets and the coarseness tended to increase in such forms to the South and to the East. In other words the tendency to exaggerate the expression of the awn character was associated with higher temperatures, lower rainfall and therefore lower relative moisture.

The awn as in barley may serve as an organ of transpiration, but no work appears to have been carried out in the case of the oat to test this hypothesis. There is no doubt, however, that it is of importance in the wild forms in serving to transport and to bury the grain. This is due to the hygroscopic action, the marked twisting and untwisting of the awn being a characteristic of all the wild forms. This is generally associated with a strongly developed callus, which may be short or long.

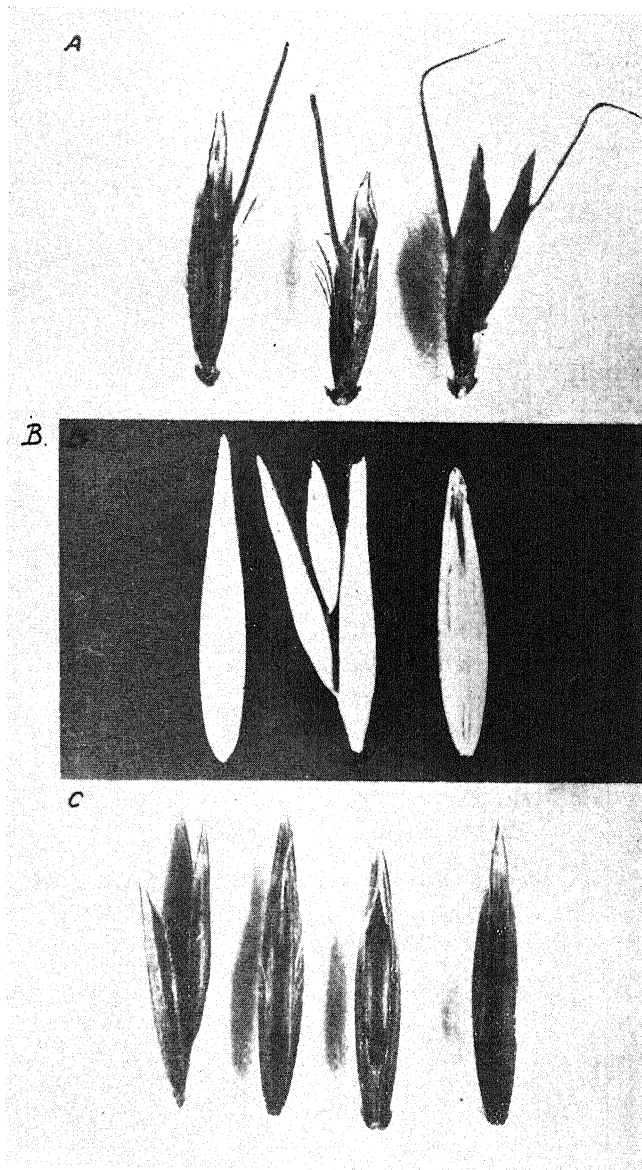


FIG. 7.

- A. Wild oats (*A. fatua*) used as a parent in crosses with selection No. 76.  
 B. Selection No. 76 (*A. sativa*) used as a parent in crosses with wild oats.  
 C.  $F_1$  from the cross between selection No. 76 and wild oats. (After Aamodt *et al.*)

The short callused forms are capable of creeping movements, penetrating readily into loose or cultivated soils. In the wild species, *A. clauda* and *A. pilosa*, which grow on more compact soils, and still more markedly in *A. longiglumis* and *A. ventricosa*, the callus becomes so elongated that the grains can be worked with the aid of the awns into relatively hard compact uncultivated soils.

The inner bract is the palea. It is thin and membranous, somewhat shorter than the lemma, two-toothed and closely invests the grain. The rachilla, except in certain "nuda" forms, is short, varying from 1.5 to 3.5 mm. It may be round, flattened or grooved; glabrous or hairy; more or less free from the lemma or partially enveloped.

There are 2 lodicules; 3 stamens; and a solitary pistil with 2 plumose styles.

**UNION OF SPIKELETS TO PEDUNCLE AND OF FLORETS TO RACHILLA.**—In most oats, the callus of the first floret and the basal segment of the rachilla are united obliquely in the lateral plane with the callus more or less dorsal and the rachilla ventral. Later, there may develop in the cleavage plane between the basal rachilla and the callus of the first floret, an oblique abscission layer. At maturity this layer disarticulates the spikelet from the peduncle producing a distinct oval cavity, the cicatrix, scar or "suckermouth" in the face of the callus. In a few the disarticulation is partly by abscission, partly by fracture. This leaves a poorly developed and more irregular cavity at the base of the lemma. Finally, the abscission layer may not develop and the solidified joint fractures. The base of the lemma is then rough and there is no cavity at the base.

The following table summarizes the position.

TABLE I.  
SPIKELET DISARTICULATION.

Type of Disarticulation.	Species.	Nature of Callus.	Nature of Scar.
I. Abscission	<i>A. strigosa</i> s.sp. <i>barbata</i> . (= <i>A. barbata</i> , Pott).	Oblong, obtuse, pilose.	Oblong.
	<i>A. strigosa</i> s.sp. <i>hirtula</i> . (= <i>A. hirtula</i> , Lagasca).	Short, more or less obtuse, seto-pilose.	Oblong-linear.
	<i>A. strigosa</i> s.sp. <i>Wiestii</i> (= <i>A. Wiestii</i> , Stendel).	Short, obtuse, seto-pilose.	Sub-ovate.
	<i>A. strigosa</i> s.sp. <i>Vaviloviana</i> (close to <i>A. Wiestii</i> ).	Short, obtuse, seto-pilose.	Sub-orbicular.
	<i>A. fatua</i> s.sp. <i>meridionalis</i> , Mal.	Short, obtuse, seto-pilose.	Oval or sub-orbicular.
	<i>A. fatua</i> s.sp. <i>septentrionalis</i> , Malz.	Short, obtuse, seto-pilose.	Oval or sub-orbicular.
	<i>A. fatua</i> s.sp. <i>fatua</i> (= <i>A. fatua</i> , L.).	Short, obtuse, seto-pilose.	Ovate or sub-orbicular.
	<i>A. fatua</i> s.sp. <i>cultiformis</i> , M.	Short, obtuse, harshly pilose.	Ovate or sub-orbicular.
	<i>A. sterilis</i> s.sp. <i>trichophylla</i> (= <i>A. trichophylla</i> , C. Koch).	Short, obtuse, seto-pilose.	Oblong or oval.

TABLE I—cont.

Type of Disarticulation.	Species.	Nature of Callus.	Nature of Scar.
2. Semi-Abscission	<i>A. sterilis</i> s.sp. <i>macrocarpa</i> (= <i>A. sterilis</i> , L. s.s.).	Short, wide and obtuse, seto-pilose.	Oblong or oval.
	<i>A. sterilis</i> s.sp. <i>Ludoviciana</i> (= <i>A. Ludoviciana</i> , Dur.).	Short, wide, obtuse, seto-pilose.	Oblong or oval.
	<i>A. sterilis</i> s.sp. <i>Byzantina</i> (in part) (= <i>A. Byzantina</i> , C. Koch).	Short, wide.	Wide, oblique, slightly concave.
	<i>A. sterilis</i> s.sp. <i>pseudo-sativa</i> .	Short, wide.	Wide, oblique, slightly concave.
3. Fracture	<i>A. strigosa</i> s.sp. <i>strigosa</i> (= <i>A. strigosa</i> Schreber).	Short and more or less square, glabrous.	Rudimentary or absent.
	<i>A. Proles brevis</i> (= <i>A. brevis</i> Roth).	Short and more or less square, glabrous.	Absent.
	<i>A. strigosa</i> s.sp. <i>Abyssinica</i> (= <i>A. Abyssinica</i> , Hoch).	Short, somewhat square, glabrous.	Absent.
	<i>A. fatua</i> s.sp. <i>macrantha</i> (and <i>proles nudata</i> ) (= <i>A. sativa</i> s.sp. <i>macrantha</i> Haeck).	Short.	Rudimentary, sub-horizontal.
	<i>A. fatua</i> s.sp. <i>nodipilosa</i> and <i>proles decorticata</i> .	Short.	Slightly rough, sub-horizontal.
	<i>A. fatua</i> sp. <i>sativa</i> and <i>proles chinensis</i> (= <i>A. sativa</i> L. and <i>A. sativa</i> v. <i>chinensis</i> Doell. and <i>A. chinensis</i> , Metzger).	Short.	Rough, sub-horizontal.
	<i>A. fatua</i> s.sp. <i>praeagravis</i> (= <i>A. sativa praeagravis</i> , Krause).	Short.	Rough, sub-horizontal.
	<i>A. sterilis</i> s.sp. <i>nodipubescens</i> .	Short.	Rough, somewhat wide, concave or smooth, strongly oblique.
	<i>A. sterilis</i> s.sp. <i>Byzantina</i> (in part) (= <i>A. Byzantina</i> , C. Koch, = <i>A. sterilis culta</i> , Marq).	Short.	Rudimentary.
	<i>A. sterilis</i> s.sp. <i>pseudo-sativa</i> .	Short.	Rudimentary.

The connection of the upper florets to the rachilla is more or less similar to the connection of the spikelet to the peduncle. Either the rachilla articulates with the callus, allowing the matured grain to disarticulate from the rachilla, which thus remains attached to the lower grain ; or the rachilla and the callus solidify, thus preventing disarticulation and causing the matured grain to fracture from the rachilla either above or below, or to produce fracture. In the first case, the lower grain will carry practically the whole of the rachilla ; in the second, only a trace of the rachilla at the base or a broken fragment will be found. On the other hand, the base of the upper grain either exhibits a small scar, or carries with it the broken rachilla, the portion being either very short, medium or wellnigh entire.

TABLE II.

## FLORET DISJUNCTION.

Type of Disjunction.	Nature of Rachilla on Basal Grain.	Nature of Base of upper Grain.	Species.
1. Disarticulation.	Basal segment of rachilla adhering vertically to basal grain.	Indistinct Scar.	<i>A. clauda</i> , Dur. <i>A. longiglumis</i> , Dur. <i>A. strigosa</i> s.sp. <i>barbata</i> ( = <i>A. barbata</i> , Pott). <i>A. strigosa</i> sp. <i>hirtula</i> ( = <i>A. hirtula</i> , L). <i>A. strigosa</i> s.sp. <i>Wiestii</i> ( = <i>A. Wiestii</i> , Steudel). <i>A. strigosa</i> sp. <i>Vaviloviana</i> , Mal. <i>A. strigosa</i> s.sp. <i>barbata</i> ( = <i>A. barbata</i> Pott). <i>A. fatua</i> s.sp. <i>septentrionalis</i> , Mal. <i>A. fatua</i> s.sp. <i>fatua</i> ( = <i>A. fatua</i> , L). <i>A. fatua</i> s.sp. <i>cultiformis</i> , Mal. (majority). <i>A. fatua</i> s.sp. <i>meridionalis</i> , Mal.
2. Fracture. a. Fracturing at the base (Basi - fracture).	Basal segment of rachilla practically absent.	No scar. Base of the grain with rachilla adhering.	<i>A. pilosa</i> , M.B. <i>A. ventricosa</i> (Balansa), Malzew. <i>A. fatua</i> s.sp. <i>sativa</i> (some varieties). <i>A. sterilis</i> s.sp. <i>trichophylla</i> .

TABLE II—cont.

Type of Disjunction.	Nature of Rachilla on basal grain.	Nature of Base of upper Grain.	Species.
b. Fracturing at the apex.	Basal segment of rachilla adhering to lower grain.	No scar.	<i>A. sterilis</i> s.sp. <i>macrocarpa</i> .
			<i>A. sterilis</i> s.sp. <i>Ludoviciana</i> .
			<i>A. sterilis</i> s.sp. <i>Byzantina</i> (= <i>A. Byzantina</i> , Koch).
			<i>A. sterilis</i> s.sp. <i>pseudo-sativa</i> .
			<i>A. sterilis</i> s.sp. <i>nodipubescens</i> , M.
			<i>A. strigosa</i> s.sp. <i>strigosa</i> (= <i>A. strigosa</i> , Schreber = <i>A. strigosa</i> proles <i>brevis</i> .)
			<i>A. fatua</i> s.sp. <i>meridionalis</i> (= <i>A. fatua meridionalis</i> , Hack).
			<i>A. fatua</i> s.sp. <i>nodipilosa</i> , Mal.
			<i>A. fatua</i> s.sp. <i>sativa</i> (many). (= <i>A. sativa</i> , L.).
			<i>A. fatua</i> s.sp. <i>praegravis</i> .
c. Hetero-fracture.	Basal segment of rachilla fractured irregularly towards the middle and adhering to lower grain.	No scar. Upper portion of fractured rachilla adhering to base of upper grain.	All above species occasionally.

Spikelet disarticulation appears to be a fairly constant character, and was used by Etheridge (1916) in his classification. Surface (1916), Love and Craig (1918) and Fraser found that the absence of the scar (as in s.sp. *sativa*) was dominant over its presence (as in s.sp. *fatua*).

Surface (1916) also reports that the presence of a marked scar on the basal grain is correlated with the following characteristics:—

1. A scar on the upper grain ;
2. Very heavy awns on the lower grain of every spikelet ;
3. Very heavy awns on the upper grains of every spikelet ;
4. Heavy pubescence on the pedicel of the lower grains ;
5. Heavy pubescence on the pedicel of the upper grain ;
6. Heavy pubescence on all sides of the base of the lower grain ;
7. Heavy pubescence on all sides of the base of the upper grain. (See Fig. 7, A.)

There are, however, exceptions.



Coffman, et al. (1925), in a study of the Burt Oat, also found that the fractured base was dominant to the scar condition. In Kherson Oats (Coffman and Stanton, 1924), disarticulation by semi-abscission was constant in some strains, but showed segregation in others. Most strains showed the rough pointed base characteristic of s.sp. *sativa*. Correlation in Burt Oats was found in the following characters:— (1) floret disjunction and spikelet disarticulation; (2) spikelet disarticulation and basal hairs; (3) spikelet disarticulation and awns; (4) lemma colour and spikelet disarticulation.

In general the work of subsequent investigators establishes the fact that in the cross *A. fatua* by *A. sativa*, the absence of the scar (and the *sativa* complex) is partially dominant. (Tschermak, 1929; Crepin, 1920 and 1927; Nishiyama, 1929; Philp, 1933; Aamodt, Johnson and Manson, 1934).

Floret disjunction behaves somewhat similarly, though it appears to be less constant in certain varieties. In Burt, the above authors found the *sativa* type predominant; the basi-fracture type suggested a cross involving multiple factors. In the strains of Kherson Oats, disarticulation predominates.

In other crosses, *A. fatua* X *A. sterilis* (Tschermak, 1929; Florell, 1931), *A. sterilis* X *sativa* (Shegalov quoted by Huskins, 1927; Tschermak, 1929; Florell, 1931; Nishiyama, 1929), *A. byzantina* X *sativa* (Fraser, 1919; Nishiyama, 1929), and *A. fatua* X *byzantina* (Florell, 1931), a similar situation is found. The difference in the grain characters is usually due to one complex of genes which are closely linked. The general conclusion may therefore be made that the *sativa* complex is partially dominant to both the *sterilis* and *fatua* complexes, whilst the *sterilis* complex is partially dominant to the *fatua*, and that these complexes seem to behave as multiple allelomorphs.

Further, the cytological investigations of Huskins (1927, 1928) and Nishiyama (1931, a and b and 1935), indicate that the specific grain characters of *sativa*, *fatua*, *sterilis* and *byzantina* may be controlled by the genes on the C-chromosome.

**ANTHESIS AND POLLINATION.**—The inflorescence as a whole opens from the base downwards. The first spikelets to flower are those about the middle of the panicle, spreading thereafter upwards and downwards. In any one spikelet, the lower flower opens first, followed by the second, third, etc. A single flower remains open for from 50 to 70 minutes and the whole panicle requires from 6 to 7 days to complete anthesis.

As in most instances the flowers definitely open, it follows that cross-pollination is possible. It appears, however, that natural cross-pollination occurs much less frequently than in wheat. Tschermak, Rimpau, Fruwirth and Pridham noted the occurrence of natural crosses. Stanton and Coffman (1924) reported an amount varying from 10 per cent. to 0.97 per cent. Griffie and Hayes (1925) found crossing in every variety studied but infrequent, varying from 0.04 per cent. in Victoria to 1.4 per cent. in Kanota. Jones (1933) found no crossing in certain varieties and a variable percentage in others. The lowest percentage was 0.003; the highest 0.33.

The explanation must lie in the fact that pollen is shed from the stamens before and during the period of flower opening. Pollination must, therefore, have been effected in the vast majority of cases before the anthers protrude. The mode of fertilization is similar to that found in wheat.

DEVELOPMENT OF THE GRAIN.—The oat grain passes through the milk-, waxy-, full-, and dead-ripe stages as in wheat, but the details of in-filtration of the endosperm by the reserve food are not known. The ovary wall becomes the pericarp, which is not so strongly developed as in wheat. There is also partial absorption of the chlorophyll layer and of the inner epidermis. The outer integument disappears; the inner constitutes the testa. A single layer of the nucellus is all that is left of that tissue. (See Figs. 20 and 21.)

MATURE GRAIN.—Except in “naked” oats, the lemma and the palea closely invest the grain. There is, however, no union between the structures. Lemma and palea together form the “hull.” The percentage of hull to grain is of importance in judging the quality of oats, and in any one variety is fairly constant for ideal conditions. It varies, however, in the same variety in any one year with the environmental factors, and also from one year to another. The following table (University of Leeds, Department of Agriculture, Bull. No. 27) gives the variation found in a few well-known varieties.

TABLE III.  
PER CENT. OF HUSK.

Variety.	1900	1901	1902	Average.	Average weight of 2,000 grns.
Abundance	24·38	26·35	24·92	25·22	73·7
Newmarket	24·79	26·68	24·89	25·45	73·3
Banner	—	—	25·57	25·57	62
Waverley	26·72	26·82	25·05	26·20	65·8
Sandy	27·54	29·71	23·21	26·49	50·5
Hamilton	28·39	29·65	23·35	27·13	53·7
Golden Giant	30·10	28·98	24·42	27·83	57·9
Tartar King	31·95	33·92	29·96	31·94	74·7
Pioneer	36·18	35·71	31·33	34·40	66·4

The above figures indicate considerable variation from year to year. Generally speaking, the hull percentage is lowest when the conditions for the variety in question are most favourable.

The basal grain of a spikelet is the largest; it has a higher per cent. of hull than the upper grains; it may be awned; its base is blunt and it carries a short rachilla, which varies in length, shape and hairiness in the different varieties. The second grain is smaller, has a lower per cent. of hull, no awn, a pointed base and may possess a rachilla or a rudimentary one only. If a third grain be present, it resembles the second but is smaller.

So-called "double-grains" may occasionally be found. They occur only in spikelets that have two grains, and are so called because the second is wholly or partly enclosed by the lemma of the first grain. Certain investigators regard these grains as a varietal characteristic. Both views are in part correct. The double-grained condition is an abnormality due to incomplete development which is more frequently found in certain varieties than in others. There is accordingly a varietal tendency towards its development.

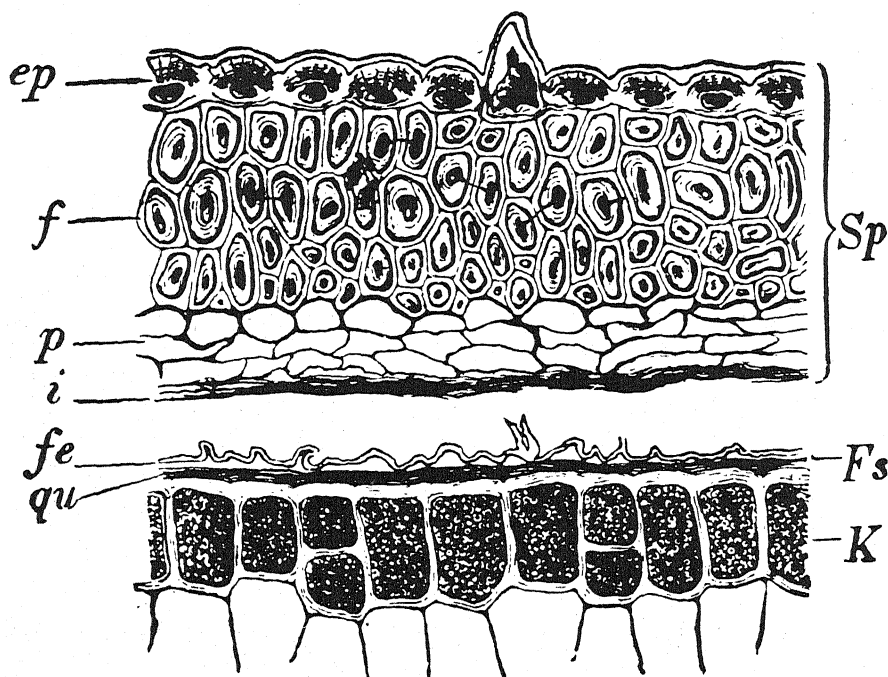


FIG. 8. Cross-section of lemma and grain of Oat.

*Sp.* lemma, consisting of *ep* outer epidermis ; *f*, hypoderm fibres ; *p*, spongy parenchyma and *i*, inner epidermis ; *Fs*, pericarp, consisting of *fe*, epicarp and *qu*, cross cells ; *K*, aleurone cells of the endosperm. X 160. (After Moeller, from Winton, *The Microscopy of Vegetable Foods*, by special permission of John Wiley and Sons, Inc.)

The true grain is elongated and carries slender hairs over the whole surface. The embryo is relatively smaller than in wheat or barley.

I. GRAIN COATS.—A. *Hull*.—a. **Lemma**.—The external characters are identical except for size with those of the young lemma of the spikelet. Structurally it shows the following four distinct layers :—

(1) Epidermis. The cells are of three types :

1. Elongated cells with thick wavy walls.
2. Small paired cells (twin-cells), one of which is generally crescent-shaped.
3. Circular cells.

On the edges and especially towards the apex, short dagger-shaped hairs, generally thick-walled and broad at the base, occur. Except at the margins, the walls of all the cells are very thick and the lumens correspondingly narrow.

(2) Hypoderm. Four to ten layers of fibres, narrow and elongated (often over 1 mm. long), with thick, almost non-porous walls. These walls next the epidermis may be toothed.

(3) Parenchyma. The parenchyma is stellate, and differentiates the lemma of the oat from that of the other cereals.

(4) Inner epidermis. The cells are elongated with thin straight walls and fairly numerous stomata.

b. *Palea*.—Similar to the above, but the hypoderm layer throughout is thinner, and is practically absent in the membranous wings. Near to and parallel with the veins are rows of stomata. On the veins, stiff thick-walled pointed hairs are found (15 to 100 mm. long). (Fig. 8, sp.)

B. *Pericarp*.—The pericarp as a whole is thin and the layers not easily differentiated.

a. Epidermis (Epicarp). The cells are thin-walled, more or less beaded and elongated, becoming almost isodiametric at the apex and base. Hairs from 1 to 2 mm. long are borne singly or in groups of 2 to 4 (or even more) over the surface, but especially the apex. These hairs tend to taper at both ends, the base being often narrower than the middle.

b. Middle parenchyma (Mesocarp). Several layers of similar elongated cells with thin walls. They become more and more disintegrated as the grain ripens.

c. Cross cells. These are the product of the chlorophyll layer. In the mature grain they form a single, often very indistinct layer of cells, set in irregular zig-zag rows.

d. Tube cells (Endocarp). The inner epidermis is strongly absorbed and is ultimately represented by a few indistinct tube cells.

C. *Testa*.—A very indistinct layer the product of the inner integument.

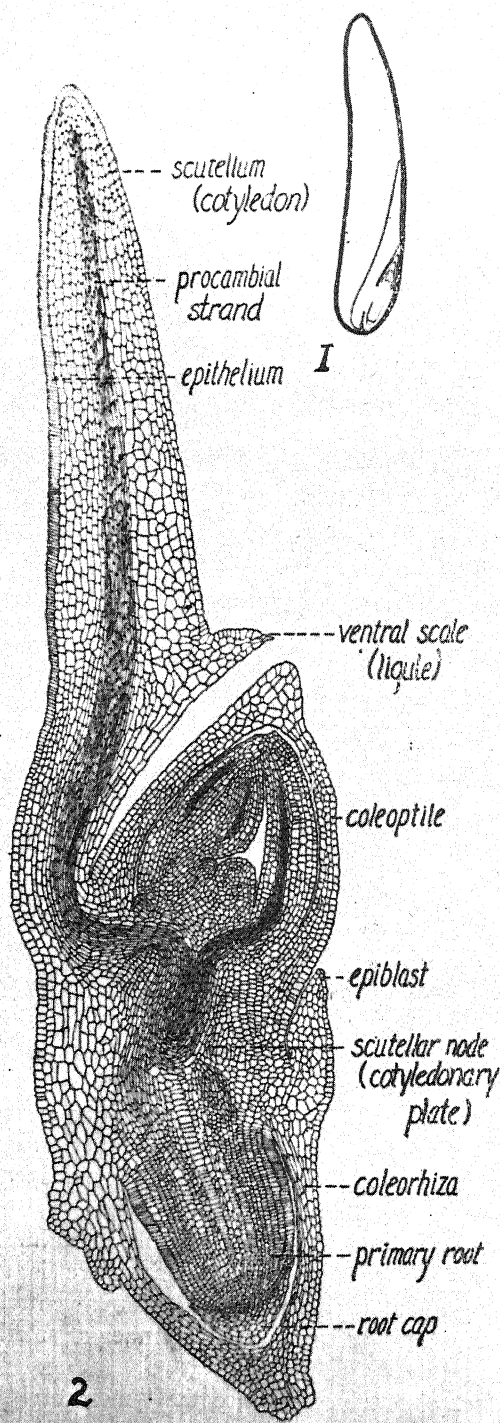
II. NUCELLAR LAYER.—(Perisperm.)—The single layer of the perisperm—all that is left of the nucellar tissue—is almost indistinguishable.

III. ENDOSPERM.—a. *Aleurone*.—The aleurone is mostly a single, at times a double layer of more or less rectangular cells whose walls are thinner than those found in wheat, barley and rye.

b. *Starch endosperm*.—The cells are large and thin-walled with numerous small polygonal starch grains. These are generally aggregated into spherical or ellipsoidal masses which readily disintegrate. Characteristic spindle-shaped grains also occur. There is no gluten in the protein. (Fig. 8.)

IV. EMBRYO.—a. *Scutellum*.—The scutellum is fleshy and leaf-like in outline, and distinctly longer than the embryonic axis. On the back there is a well-developed dorsal ridge, and between the plumule and the scutellum a ventral scale. A single scutellar bundle runs upwards and gives off a number of small branches which diverge from the apex.

b. *Plumule*.—This is inserted directly on the axis, since the “mesocotyl” before germination is very short. On germination, the “mesocotyl” is the first



part to elongate along with the radicle and soon the insertion of the coleoptile is raised above the scutellar insertion on a definite axis. The plumule as a whole is covered by the coleoptile, and several rudimentary leaves are pre-formed.

c. *Radicle*.—The radicle consists of a single primary seminal root with at least two secondaries pre-formed. These are inserted just below the divergence of the coleoptile. A third rootlet may appear later, at a level immediately above the divergence of the coleoptile. The whole radicle is enclosed in the coleorhiza.

d. *Epiblast*.—There is a well-developed scale-like epiblast inserted on the ventral face of the embryo. (Fig. 9.)

**CHROMOSOME NUMBERS.**—The chromosome numbers of several species of *Avena* (including all the cultivated species) have been studied in recent years by Kihara (1919 and 1924); Nikolaewa (1922); Stolze (1925); Dorsey (1925); Winge (1925); Huskins (1925); Goulden (1926); Stanton and Dorsey (1927); Nishiyama (1929); Stahlin (1930); Emme (1930) and others.

FIG. 9.

1. Diagram of the caryopsis in longitudinal section, showing the position of the embryo.

2. Longitudinal section of the embryo of *Avena*. (After Avery.)

In all cases examined the cytological behaviour is similar to that of normal diploid species (Huskins, 1927).

The *Euavena* species fall naturally into three groups, with 7, 14 and 21 haploid chromosomes respectively. Until recently, the chromosome numbers reported for certain of the forms in the first and second group appeared to conflict with their morphological characteristics and their geographical distribution. (Figs. 10, 11, 13 and 14.)

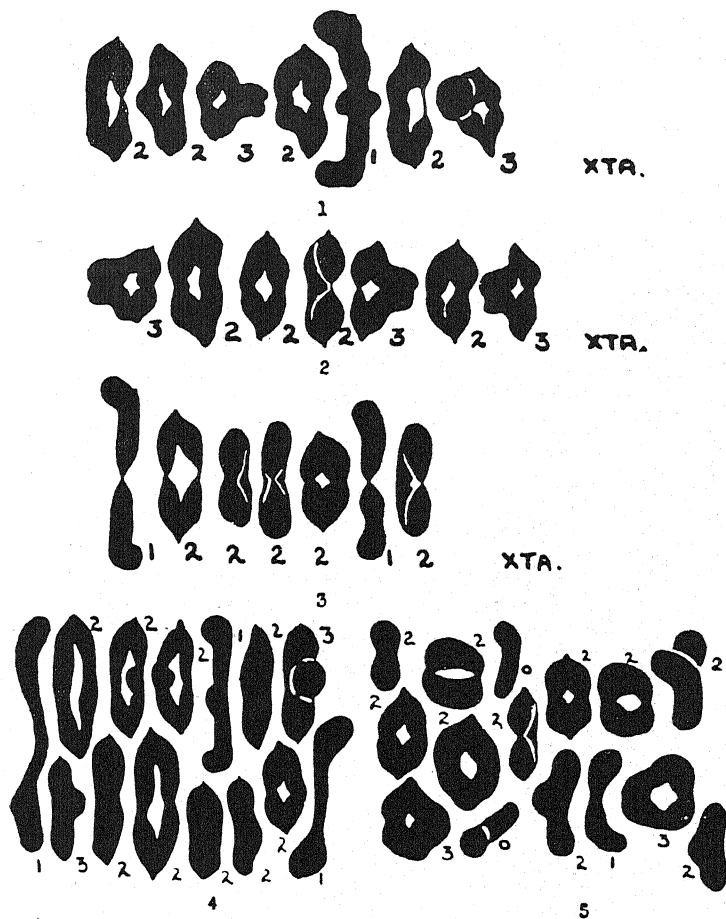


FIG. 10. Metaphase stage of first maturation divisions in Oat species. Figures beside bivalents indicate numbers of chiasmata.

1. *A. strigosa* Schreb ; 2. *A. brevis* Roth. ; 3. *A. Wiestii* Steudel ; 4. *A. barbata* Pott ; 5. *A. abyssinica* Hochst ("naine"). X 2600. (After Spier.)

The recent systematic work of Malzew (1930), and the cytological work of Emme (1930), however, indicate that the discrepancies previously found were probably due to incorrect determinations. Thus s.sp. *hirtula*, s.sp. *strigosa* (including proles *brevis*) and s.sp. *nuda* of *A. strigosa* (L) Malzew, have in reality 7/14 chromosomes and are allied in many respects to the other four species

with 7/14 chromosomes. *S.sp. barbata* has 14/28 chromosomes though Kihara (1924) believed that he obtained a 7/14 chromosome form of *barbata*; Love also secured a similar type with 7/14 chromosomes, though he states that the form was "obtained as *barbata* but looks like *strigosa*." Emme is of the opinion that these forms were in reality specimens of s.sp. *strigosa*.



FIG. 11. First meiotic division in Oat species.

1. *A. sterilis* L. (parent of 5x hybrid); 2. *A. sterilis* L. (parent of 6x hybrid); 3. *A. sativa* L. var. Radnorshire sprig; 4. 6x hybrid. a. 21 bivalents of one-spore mother cell; b. quadrivalent configurations. X 2600. (After Spier.)

The form *A. Wiestii* has also been reported as having 7/14 chromosomes. Again, Emme (l.c) casts doubt on the correctness of the identification. In certain of its environmental forms, this species is incorporated by Malzew in s.sp. *Vaviloviana* (with 14/28 chromosomes), and the type form is regarded by Vavilov as akin to s.sp. *hirtula*, though possessing a different geographical distribution. Malzew has accordingly included all 7/14 forms of *Wiestii* in s.sp. *hirtula*.

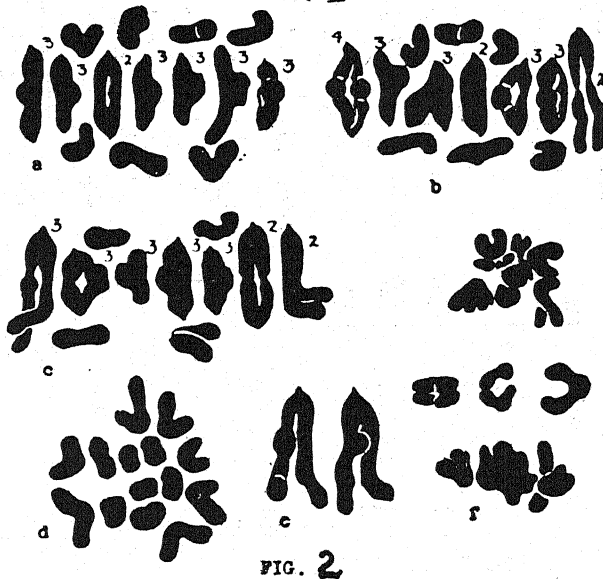
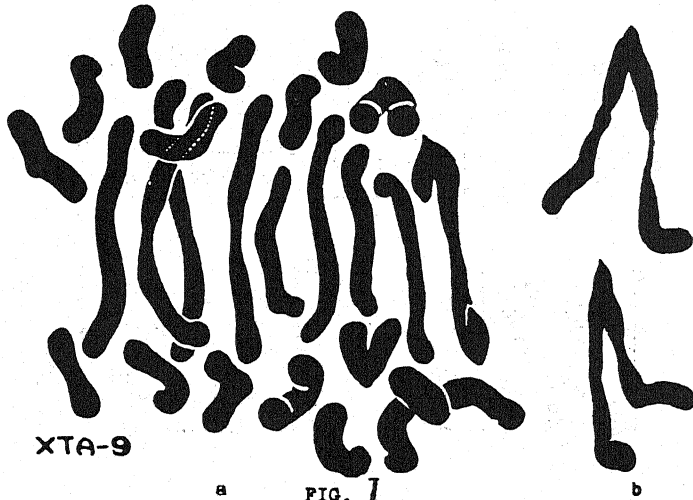


FIG. 12. First meiotic division in Oat hybrids.

1. 5x hybrid; a. 9 bivalents; 17 univalents of one cell; b. trivalent configurations.
2. 3x hybrid; a. 7 univalents, 7 bivalents; b. 6 univalents, 6 bivalents, 1 trivalent; c. 5 univalents, 5 bivalents, 2 trivalents; d. polar view showing peripheral position of the 7 univalents; e. typical trivalents with one chromosome showing two chiasmata in one arm, and one chiasma in the other arm; f. equational division of lagging univalents. X. 2600. (After Spier.)



TABLE IV.—CYTOLOGICAL RELATIONSHIPS OF THE SPECIES OF EU-AVENA. (After Malzew, modified.)

SUB-SECTION ARISTULAE.		SUB-SECTION DENTICULATAE.	
SERIES : 1. INAEQUALIGLUMIS TOMOSOMES : 2X = 14	SERIES : 2. STIPITATAE 2X = 14	SERIES : 3. EURBATABAE 4X = 28	6X = 42.
(Cultivated "nuda(forms.")	nuda ↑	dearorticata nudata ↑	chinensis (= A. sativa chinensis) and (A = chinensis) ↑
(cultivated.)	Strigosa incl. brevis (= A. strigosa and A. brevis) ↑	nodipilosa macrantha ↑	sativa (= A. sativa) ↑
(non-cultivated.)	hirtula = (A. Wiestii in part) ↑	abyssinica ↑	pseudo sativa ↑
l. clauda, Dur.	3. A. longiglumis, Dur	barbata Wiestii (= A. Wiestii in part) ↑	nodipubes- cens ↑
4. pilosa, M.B.	4. A. ventricosa (Balansa), Malz.	Vaniloo- iana ↑	byzantina = A. byzantina (A. sterilis cultiformis) ↑
		Septen- trionalis ↑	Ludoviciana tricho- phylla ↑
		fatua (A. fatua, L.) ↑	macrocarpa ↑
		6. A. fatua (L.), Malz.	7. A. sterilis (L.), Malz.
		5. A. strigosa, (Schreb.) Malz. (→)	

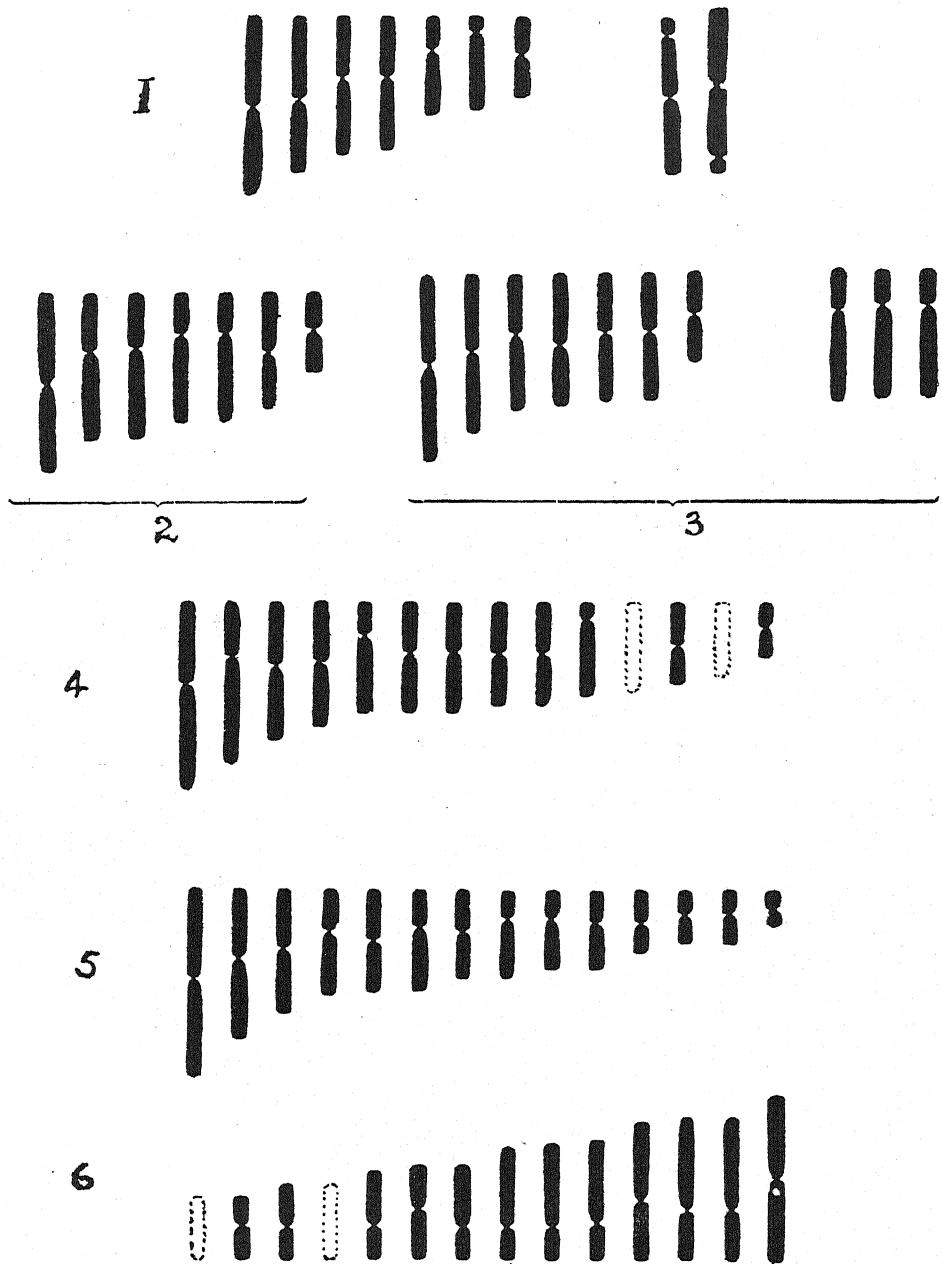


FIG. 13. Karyotypes of Avena Spp.

1. *S.sp strigosa* (s.s.) 7 chromosomes and the main variants of chromosomes 1 and 2.
2. *Proles nuda*.
3. *Proles brevis*. Variants of 3 longest chromosomes.
4. *S.sp. barbata*.
5. *S.sp. Vaviloviana*.
6. *S.sp. abyssinica*. (After Emme.)

In table IV, it will be seen that four wild species and the *hirtula strigosa* forms have  $7/14$  chromosomes. They constitute a fairly compact group also from both the morphological and geographical standpoint. The second group with  $14/28$  chromosomes consists of the remainder of the *strigosa* forms. They, too, are closely related. The third group with  $21/42$  chromosomes includes all forms of *A. fatua* (*sensu ampl.*) and *A. sterilis* (*sensu ampl.*).

(See Figs. 10 to 14.)

**GERMINATION AND THE SEEDLING.**—The so-called maximum, minimum and optimum temperatures for the germination of oats are practically the same as for wheat.

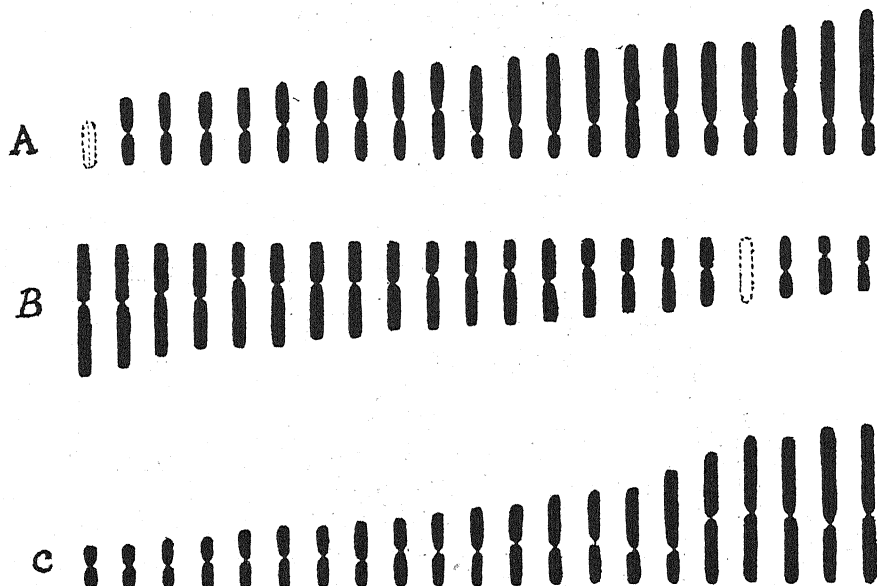


FIG. 14. Karyotypes of *Avena* Spp.

- A. *Sp. diffusa*. var. *mutica* f. *gigantea*.
- B. *Sp. byzantina*.
- C. *Ssp. Ludoviciana*. (After Emme.)

The coleorhiza appears early as a white glistening knob at the basal end. It is almost immediately ruptured by the primary seminal root which thereafter elongates rapidly. Later, a pair of laterals emerge, followed in most cases by a second pair.

The plumule appears some time after the appearance of the primary root, a delay caused by the fact that the plumule is unable to break through the hull and is forced to grow upwards beneath the lemma. The time of the appearance of the coleoptile above ground again depends on the depth of the planting. In normally planted grain, the coleoptile node is raised through the elongation of the so-called "mesocotyl" to a point just below ground level. (Fig. 17.)

The first leaf to appear is twisted; the remainder are normal. All the leaves are longer and more tapering than in wheat. The sheaths are sparsely

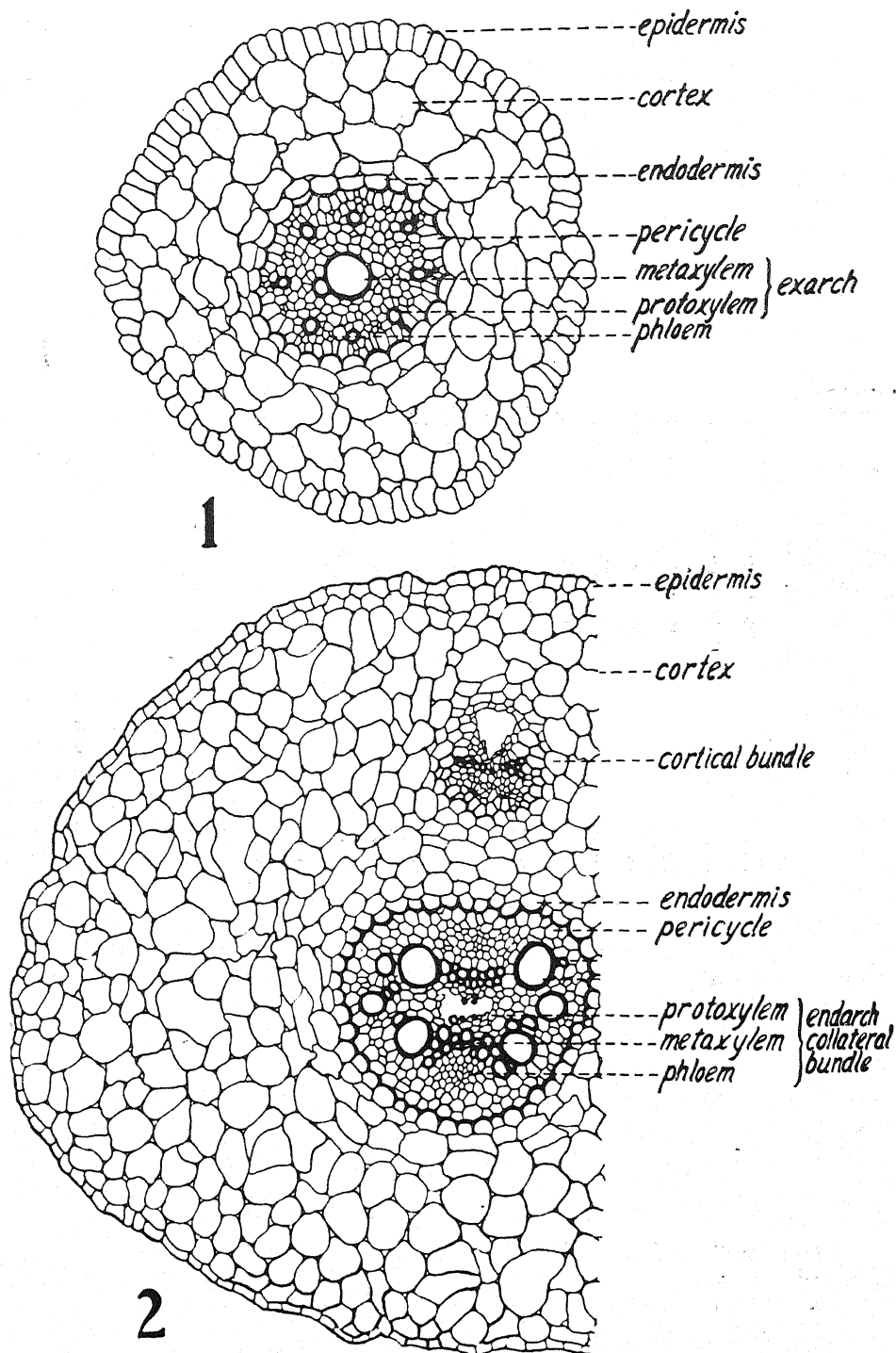


FIG. 15.

1. Transverse section of primary root of seedling; 2. Transverse section of first

hairy or glabrous ; the collar is broad, clearly divided into two parts by the mid-rib, finely hairy and without auricles ; the ligule (absent in some varieties) is membranous, long and acute toothed ; the blades are broad and flat, often hairy along the margins. In some, the early growth is compact and erect ; in others definitely prostrate, in a few semi-prostrate.

Growth of the first adventitious roots commences just before the lateral buds begin to develop as tillers.

**SEEDLING ANATOMY.**—*Seminal roots.*—The outer surface is covered by a single layer of somewhat elongated epidermal cells, their outer-tangential walls being slightly cutinized. At an early date, this epidermis is sloughed and the adjacent cells of the cortex take its place, becoming at the same time conspicuously thickened. This cortex is comparatively wide, and consists of somewhat irregular thin-walled cells with inter-cellular spaces. The endodermis is distinct with the inner tangential walls thickened. Within the stele, there is a single pericyclic layer. The centre is occupied by a large vessel, usually referred to as metaxylem, but differentiating at the same time as or before the protoxylem. It is surrounded by parenchyma but may be accompanied by one or more smaller vessels. The number of protoxylem points is generally 7 to 8. The alternating phloem is indistinct. (Fig. 15.)

*Axis.*—The meristematic region of the axis is above the scutellar plate, surrounding the scutellar bundle as elongation takes place ; the scutellar bundle accordingly extends upwards within the axis, but remains free from the stele until it approaches the level of the divergence of the coleoptile.

The first change from the exarch to the endarch condition takes place in the vascular plate at the scutellar node. As development proceeds, the downward differentiation is typical root ; the upward differentiation is stem-like. Between the level of the divergence of the scutellum and that of the coleoptile, the stele is transitional. There are two prominent endarch collateral bundles situated opposite to one another, with their protoxylem directed towards the centre. In origin, they are one and the same bundle and may be traced back to the scutellum. On either side of each collateral bundle there are 3 or 4 groups of protoxylem and metaxylem, exhibiting varying degrees of exarch and endarch structure. A large inter-cellular space often occupies the centre. (Fig. 15 (2).)

Outside the stele, the scutellar bundle—the so-called cortical bundle—is conspicuous. (Fig. 15 (2).) At the level of divergence of the coleoptile, it enters the stele and turns downwards within it. According to Avery (1930), it previously gives rise to two branches which extend first laterally and then upwards. Each in turn divides, one branch of each entering and forming a coleoptile bundle. According to Sargent and Arber (1915), half of each coleoptile bundle arises from the stele.

The inter-node between the coleoptile and the first true foliage leaf is also more or less “transitional.” The cortex is wide, the vascular bundles poorly differentiated and an abundance of procambium is present, here and there differentiated into xylem and phloem. (Fig. 16 (1).) The subsequent inter-node is still more stem-like, although the endarch arrangement is not complete (Avery, 1930). (Fig. 16 (2).)

According to McCall (1934), the cross-axis procambial plate which separates

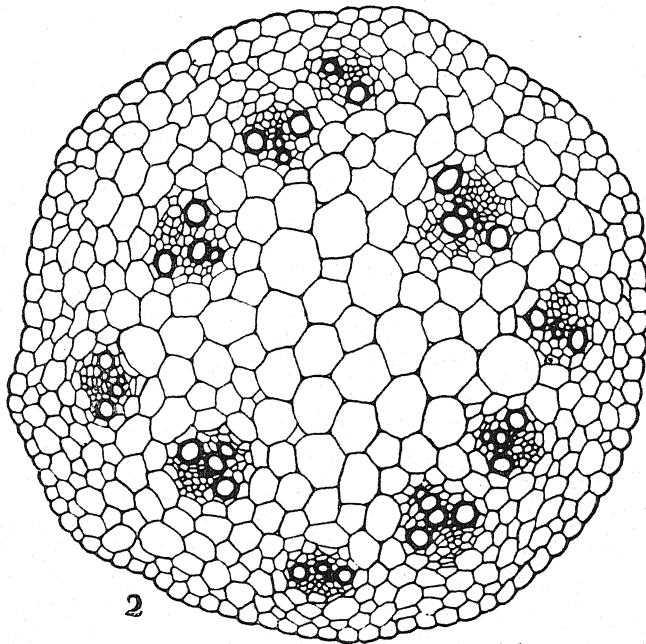
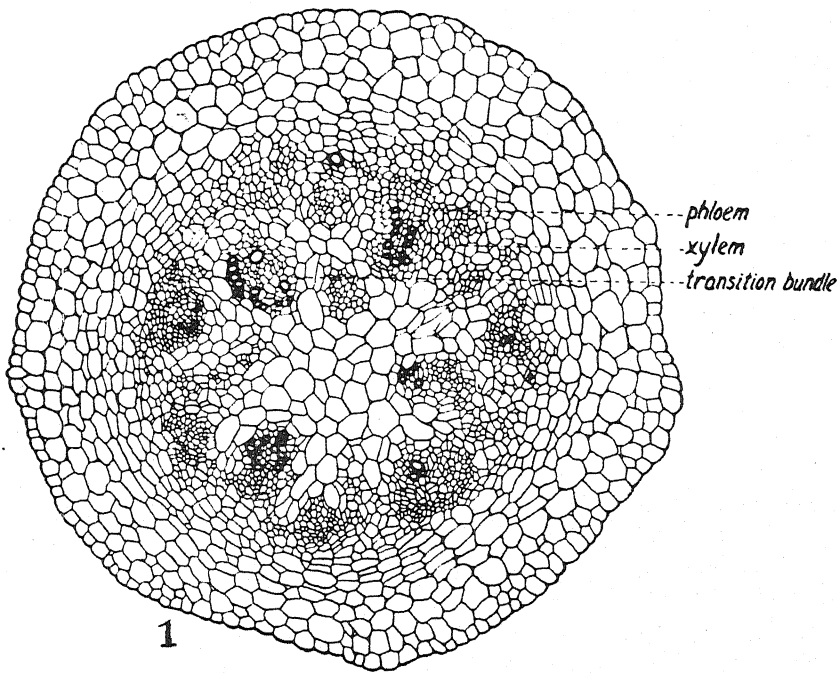


FIG. 16.

1. Transverse section of second inter-node of four-weeks-old plant ; 2. Transverse section of third inter-node of six-weeks-old plant. (After Avery.)

the primary root and stem of the embryo is in reality the first node. The scutellum accordingly diverges from the second node and the coleoptile from the third. Now in *Avena*, intercalary growth during germination and early seedling development is mainly confined to the first inter-node. (Fig. 18 (A).) This involves the entire section of the axis, including the scutellum trace in the axis, but not the scutellum itself. As a consequence of the elongation of this first inter-node, the second node and with it the scutellum trace is carried above the attachment of the scutellum to the axis, thus leading to the formation of an inverted scutellar trace,

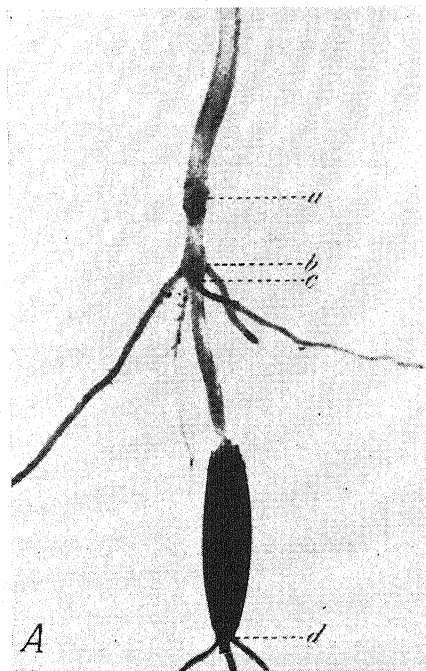


FIG. 17. Sub-crown region of fourteen-day-old oat seedling.  $\times 2\frac{1}{2}$ .

- a.* Fourth node, crown node; *b.* Third node, coleoptile divergence; *c.* Second node, scutellum-trace divergence; *d.* First node, transition from root to stem. (After McCall.)

growing downwards to connect with the scutellum. On this interpretation the so-called "mesocotyl" is hypocotyl. (Figs. 17 and 18 (A).)

The second inter-node in *Avena* shows but little elongation and as a consequence the second and third nodes remain close to one another. (Figs. 17 and 18 (A).)\*

The coleoptile is similar to that of maize but is much smaller. The two bundles are situated laterally. Each bundle is small, with few xylem groups and relatively abundant phloem. There is almost universally a bud in its axil (Avery, 1930).

\* McCall's interpretation has been criticized by Boyd and Avery (Bot. Gaz. 97: 1936). They regard the first inter-node as the region extending from the cotyledonary to the coleoptilar node.

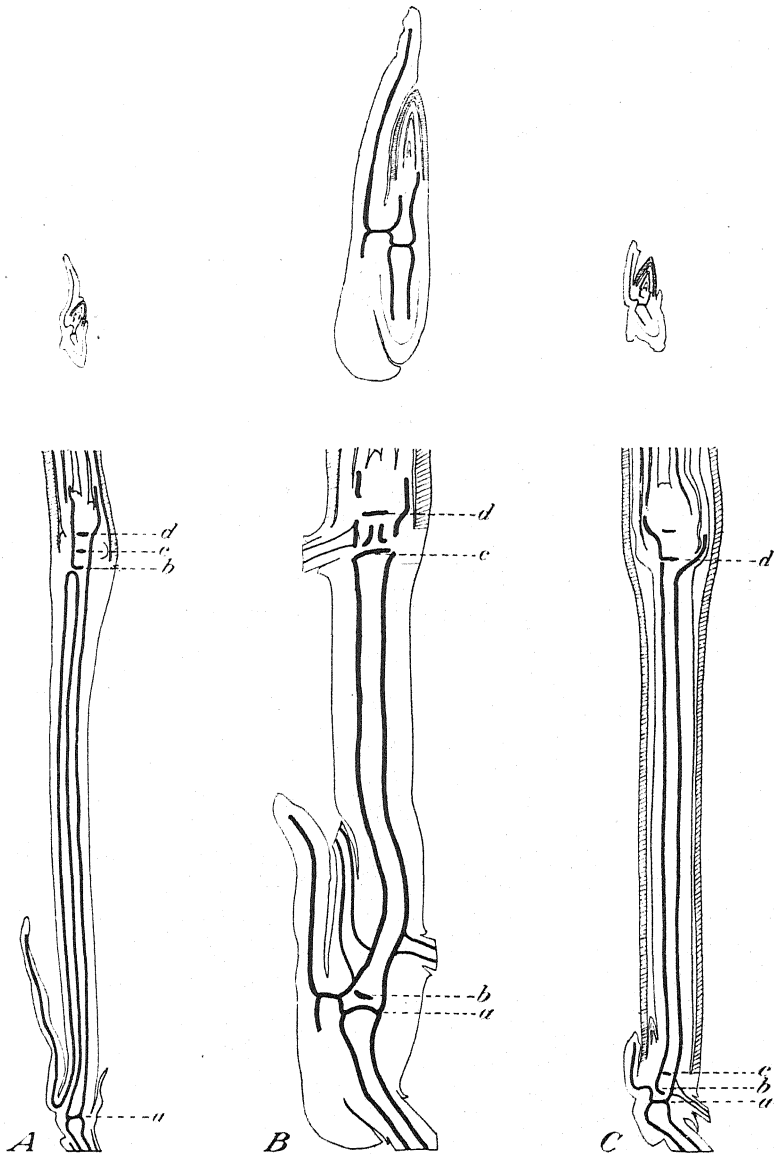


FIG. 18. Diagrammatic sagittal view of the embryos (above) and the sub-crown region (below) of oat, corn, and wheat seedlings, showing vascular and nodal relationships and the differences in intercalary growth during germination in the three genera. X 4. *A*, Oat (*Avena sativa* var. Iogold): *a*, First node, transition from root to stem; *b*, second node, scutellum-trace divergence; *c*, third node, coleoptile divergence; *d*, fourth node. *B*, Corn (*Zea mays* var. Garrick): Designations the same as in *A*. *C*, Wheat (*Triticum vulgare* var. Turkey): Designations the same as in *A*. (After McCall.)



*Leaves*.—The later foliage leaves are very similar to those of wheat. The mesophyll consists of closely arranged cells, and the palisade layer is indistinct. The vascular bundles are approximately equal in size, except at the mid-rib. The bundle sheaths are small and the cells contain no chlorophyll. Sclerenchymatous cells are well developed at the mid-rib; elsewhere they are limited, consisting of a few cells in both epidermal layers opposite the bundles. Compared with wheat, the motor-cells are small (Avery, 1930).

**CLASSIFICATION**.—The cultivated races of oats all fall into the section *Euavena* (Griseb) of the genus *Avena* (Tournefort, 1700). Many classifications have been attempted, the more important being those of Link (1827 and 1829), Lejune and Courtois (1828), Koch (1837 and 1844), Casson (1854), Jessen (1863), Alefield (1866), Körnecke and Werner (1885), Haussknecht (1885, 1892, 1894, 1899), C. Koch (1888), Atterberg (1891), Wilson (1901), Denaffe and Siderot (1902), Bohmer (1908–09), Raum (1909), Thellung (1911, 1913, 1918, 1928), Etheridge (1916), Zade (1918), Marquand (1922), Archer et al. (1922), and Hunter (1924).

In all these classifications, the differentiation of the main types is unsatisfactory, though the phylogenetic inter-relationships become clearer in the work of Haussknecht (l.c), Trabut (1911) and Thellung (l.c). Identification of the more important cultivated varieties is also rendered possible in the more recent memoirs (for American varieties, Etheridge (1916); English varieties, Marquand (1921) and Hunter (1929); Australian varieties, Archer et al. (1924); South African varieties, de Villiers and Sim (1930)).

The following classification (based on that of Etheridge) analyses the species as they are generally accepted and referred to in the English-speaking countries.

#### SYNOPSIS OF SPECIES.

##### Group 1.

Grain entirely free from lemma and palea; glumes and lemma alike in texture . . . . .

*A. nuda*, L.

##### Group 2.

Grains firmly enclosed by lemma and palea; glumes and lemma different in texture.

A. Spikelets disarticulating by abscission.

B. Floret disjunction by disarticulation.

C. Lemma without awn points . . . . .

*A. fatua*, L.

CC. Lemma with awn points.

D. Lemma densely hairy; awns long . . . . .

*A. barbata*, Pott.

DD. Lemma less hairy; awns shorter : . . . . .

*A. Wiestii*, Steudel.

BB. Floret disjunction by fracture . . . . .

*A. sterilis*, L.

AA. Spikelets disarticulating by semi-abscission . . . . .

*A. Byzantina*, Koch.

( = cultivated *A. sterilis*)

AAA. Spikelets disarticulating by fracture.

B. Lemma with veins projecting as tooth or awn points.

C. Lemma with 4 tooth or awn points . *A. abyssinica*, Hochst

CC. Lemma with 2 tooth or awn points.

D. Lemma elongate, lanceolate with distinct awn points . . . *A. strigosa*, Schreb.

DD. Lemma short, abrupt, blunt with very short awn points . . . *A. brevis*, Roth.

BB. Lemma without tooth or awn points.

C. Panicles more or less equilateral ; spreading . . . *A. sativa*, L.

CC. Panicles equilateral ; appressed . *A. orientalis*, Schr.

The above classification is defective in several respects. In the first instance, it makes *A. nuda*, L (= *A. sativa chinensis*) a separate species, when in fact the "nuda" type is but another instance of parallel variation, and may find expression in any of the species. Secondly, it obscures the phylogeny, and is not in alignment with the chromosome numbers. Also, certain of the species are too vague and based on insufficient material.

These objections do not hold to the same extent for the recent classification of Malzew (1930), which is here given as an alternative. Its rigid adherence to systematic nomenclature, however, renders it cumbersome for the differentiation of the economic varieties.

Malzew recognizes seven fundamental species, viz., *A. clauda*, Dur. ; *A. pilosa*, M.B. ; *A. longiglumis*, Dur. ; *A. ventricosa* (Balansa), Malz. ; *A. strigosa* (Schreb.), Malz. ; *A. fatua* (L.), Malz. ; *A. sterilis* (L.), Malz. The four last species are employed *sensu ampl.* These species are grouped into two sub-sections ; Aristulatae with the apex of the lemma biaristulate and the chromosome number either 14 or 28 ; Denticulatae with the apex of the lemma bidentate and the chromosome number 42. The members of the first sub-section are then arranged in three groups according to the nature of the glumes, the callus and the chromosome number.

## I. SYNOPSIS OF SPECIES OF EUAVENA.

(According to Malzew)

Sub-Section I. Aristulatae. Lemma with apex biaristulate.

Chromosomes 14/28.

Ser. 1. Inaequaliglumis.

Glumes strongly unequal, the lower shorter by one half ; callus elongated, linear, 3 mm. long ; chromosomes 14.

Species 1. *A. clauda*, Dur.

Species 2. *A. pilosa*, M.B.

Ser. 2. Stipitatae.

Glumes sub-equal or sub-unequal ; callus very long, awl-shaped, 5 to 10 mm. ; chromosomes 14.

Species 3. *A. longiglumis*, Dur.

Species 4. *A. ventricosa* (Balansa) *s. ampl.*

## Ser. 3. Eubarbata.

Glumes sub-equal, obtuse or obtusely curved; callus short or oblong, 2 mm.; chromosomes 14/28.

Species 5. *A. strigosa*, Schreb. s. *ampl.*

## Sub-Section II. Denticulatae. Lemma with apex bidentate.

Chromosomes 42.

Species 6. *A. fatua*, L. s. *ampl.*

Species 7. *A. sterilis*, L. s. *ampl.*

## II. KEY TO SPECIES OF SUB-SECTION ARISTULATAE.

## Series I. Inaequaliglumis.

A. All flowers articulate and readily falling . . . . . *A. clauda*, Dur.

AA. Only the basal flowers articulate, the upper non-articulate . . . . . *A. pilosa*, M.B.

## Series II. Stipitatae.

A. All flowers articulate and falling readily . . . . . *A. longiglumis*, Dur.

AA. Only the basal flowers articulate, the upper flowers non-articulate . . . . . *A. ventricosa* (Balansa), Mal.

Series III. Eubarbatae . . . . . *A. strigosa* (Schreb), Mal.

IIA. Key to Sub-Species of *A. STRIGOSA*, Mal.

A. All flowers articulate, disarticulating readily, spontaneous or sub-spontaneous.

B. Lemma with 2 setiform aristulae; no lateral teeth; glumes 9- to 10-nerved . . . . . s.sp. *barbata*.

BB. Lemma with 2 setiform aristulae and 1 to 2 lateral teeth; glumes 7- to 9-nerved.

C. Lemma with 2 distinct aristulae and 1 lateral tooth; cicatrix of callus oblong-linear . . . . . s.sp. *hirtula*.

CC. Lemma with 2 small aristulae and 2 lateral teeth; cicatrix of callus sub-ovate or sub-orbiculate.

D. Aristulae of lemma, 3 to 6 mm. long . . . . . s.sp. *Wiestii*.

DD. Aristulae of lemma  $\pm$  1 mm. . . . . s.sp. *Vaviloviana*.

AA. All flowers non-articulate and disarticulating by fracture. Mostly cultivated.

B. Caryopsis enclosed.

C. Lemma with 2 aristulae and 1 lateral tooth; aristulae protruding beyond or equal to the glumes.

D. Spikelets large, glumes 15 to 25 mm. long . . . . .

s.sp. *strigosa*.  
proles *brevis*.

DD. Spikelets small, glumes 12 mm. long.

- CC. Lemma biarticulate, bidentate ; aristulae  
shorter than glumes . . . . . s.sp. *abyssinica*.  
BB. Caryopsis naked . . . . . proles *nuda*.

### III. KEY TO SPECIES AND SUB-SPECIES OF DENTICULATAE.

- I. All flowers articulate and ultimately falling, scar oval or suborbiculate, except in the cultivated forms where all the flowers are non-articulate with the rachis, (generally) fracturing above and leaving the rachilla attached to the basal grain, area of fracture rudimentary, sub-horizontal . . . *A. fatua* (L), Malz.
- A. All flowers (rarely only the lower) articulate and falling readily. Plants sub-spontaneous or spontaneous.
- B. Glumes up to 30 mm. long, lemma up to 25 . . . s.sp. *meridionalis*.
- BB. Glumes up to 25 mm. long, lemma up to 20.
- C. Culms with pubescent nodes . . . ss. *septentrionalis*.
- CC. Culms with glabrous nodes.
- D. Lemma lanceolate, grains fusiform, 1.5 to 2 mm. broad ; lower sheaths pubescent . . . s.sp. *fatua*.
- DD. Lemma ovate-lanceolate, grain sub-oval or oblong, 2 to 3 mm. broad ; sheaths glabrous . . . s.sp. *cultiformis*.
- AA. All flowers non-articulate and disarticulating by fracture. Cultivated forms.
- B. Glumes elongate about 30 mm. long.
- C. Caryopsis enclosed . . . s.sp. *macrantha*.
- CC. Caryopsis naked . . . proles *nudata*.
- BB. Glumes up to 25 mm. long.
- C. Nodes pubescent.
- D. Caryopsis enclosed . . . s.sp. *nodipilosa*.
- DD. Caryopsis naked . . . proles *decorticata*.
- CC. Nodes glabrous.
- D. Lemma lanceolate, grain fusiform, caryopsis 8 mm. long.
- E. Caryopsis enclosed . . . s.sp. *sativa*.
- EE. Caryopsis naked . . . Proles *chinensis*.
- DD. Lemma ovate-lanceolate, grains sub-oval or oblong, thickened ; caryopsis 10 to 11 mm. long.
- E. Caryopsis enclosed . . . s.sp. *praeagravis*.
- EE. Caryopsis naked . . . proles *grandiuscula*.

II. Only the lower flower articulates, with the scar oblong or oval, except in the cultivated forms, where all the flowers are non-articulate with the rachis (generally) fracturing below and leaving the rachilla attached to the upper grain ; area of fracture generally strongly oblique (about 45°) and slightly concave . . . . .

*A. sterilis* (L), Mal.

A. Lower flower articulate, upper non-articulate and disarticulating in time by fracture ; spontaneous or sub-spontaneous forms.

B. Culms with pubescent nodes . . . . . *s.sp. trichophylla.*

BB. Culms with glabrous nodes.

C. Spikelets very large to large, 3- to 5-flowered, glumes 30 to 50 mm. long, lemma of lower flower, 25 to 40 mm. long . . . . . *s.sp. macrocarpa.*

CC. Spikelets large to small, 2- rarely 3-flowered, glumes 25 mm. long, lemma of lower flower 20 mm. long . . . . . *s.sp. Ludoviciana.*

AA. All flowers non-articulate and disarticulating by fracture. Cultivated or occurring in the fields.

B. Culms with pubescent nodes . . . . . *s.sp. nodipubescens.*

BB. Culms with glabrous nodes.

C. Spikelets large ; 3- (4)-flowered ; glumes  $\pm$  30 mm. long, lemma of inferior flower  $\pm$  25 mm. long ; Panicle few-flowered and shortened.

D. Caryopsis enclosed . . . . . *s.sp. byzantina.*

DD. Caryopsis naked . . . . . *proles demudata.*

CC. Spikelets small, 2-flowered ; glumes  $\pm$  25 mm. long ; lemma of inferior flower  $\pm$  20 mm. long ; panicle elongated and many-flowered . . . . . *s.sp. pseudo-sativa.*

#### DESCRIPTION OF SPECIES AND SUB-SPECIES IN SUB-SECTION ARISTULATAE.

- I. *A. clauda*, Dur. A wild species found in N. Africa, Asia Minor, Mesopotamia, Transcaucasia and East to Turkestan. The chromosome number is 7/14.
- II. *A. pilosa*, M.B. A second wild species with a somewhat similar distribution to the above (N. Africa, Asia Minor, Syria, Caucasus, and East as far as Turcomania). Chromosome number 7/14.
- III. *A. longiglumis*, Dur. (= *A. longighumis*, Richter ; *A. barbata* v. *longiglumis*, Haussknecht ; *A. barbata* v. *longighumis*, Asch. et Graebner). A wild species of the Mediterranean region (*s. strictu*) with 7/14 chromosomes.
- IV. *A. ventricosa*, Balansa, *s. ampl.*, Mal. A non-cultivated species from N. Africa and Transcaucasia, with 7/14 chromosomes. It is divided by Malzew into 2 sub-species : 1 *s.sp. ventricosa* (Balansa) from Algeria and

Cyprus (introduced) and 2 s.sp. *Bruhnsiana* (Gruner) from E. Transcaucasia.

- V. *A. strigosa*, Schreb., s. *ampl.*, Malz. This species incorporates six sub-species with two "proles."

#### NON-CULTIVATED FORMS OF STRIGOSA.

1. *A. strigosa* s.sp. *barbata* (Pott) Thell = (*A. barbata*, Pott). A non-cultivated species with 28 chromosomes. Culms ascending and finally caespitose. Leaves and sheaths generally ciliate-pubescent: Panicle more or less open or sub-second. Spikelets rather large to large, 2 to 3 (4) flowers, all aristulate: glumes sub-equal, extending slightly beyond the flowers, 9- to 10-nerved, 15 to 30 mm. long: flowers all articulate and falling: rachis very pilose: lemma generally somewhat pilose on the lower half of the back, with the apex produced in two fine awns, 5 mm. long and not exceeding the glumes; dorsal awn geniculate: callus oblong-obtuse, seto-pilose with oblong scar.

Distribution: Canary Islands and Azores; Med. region inclusive, Palestine, Syria, A. Minor, Tauria, Transcaucasia, Persia, Turcomania and East towards S. Turkestan, N. Afghanistan and W. Himalayas. Introduced into Europe, S. Africa, N. America and Japan.

Malzew describes 2 varieties and 3 sub-varieties.

2. *A. Strigosa* s.sp. *hirtula*, Lagasca. A non-cultivated 14-chromosome type intermediate between s.s. *barbata* and s.s. *Wiestii* and often confused with them.

Distribution: Mediterranean from Spain through Morocco, Algeria, Tunis, Sardinia, Sicily and East towards W. Palestine.

Four sub-varieties are known.

3. *A. strigosa* s.sp. *Wiestii* (Steud) Thill. (= *A. Wiestii*, Steud.). A non-cultivated semi-arid species with 28 chromosomes. Culms ascending, rarely sub-erect, caespitose. Leaves and sheaths softly pubescent. Panicle sub-contracted, rarely sub-second to second. Spikelets small to rarely medium, generally 2-flowered; glumes sub-equal, exceeding the flowers, 7- (8)-nerved, 15.25 mm. long; flowers all articulate and falling; rachilla pilose; lemma with the back almost to the apex slightly pilose, the apex drawn out in 2 awn points, 3 to 6 mm. long, not exceeding the glumes, and with 2 lateral teeth; callus short, obtuse, seto-pilose with sub-ovate scar.

Distribution: N.E. Africa, Egypt, Arabia, Palestine, Syria, Mesopotamia, E. Transcaucasia.

4. *A. strigosa* s.sp. *Vaviloviana*, Malz. A non-cultivated species with 28 chromosomes, closely allied to *Wiestii* and differing mainly by the exceedingly short awn points ( $\pm 1$  mm.), and its distribution (Abyssinia and Eritrea).

#### CULTIVATED FORMS OF STRIGOSA.

5. *A. strigosa* s.sp. *strigosa* (Schreb.) Thell. A 14-chromosome type rarely cultivated and closely allied to *A. hirtula* s.sp. Generally found as a weed in fields of s.sp. *sativa*. Culms erect, often rimy, with the node generally red.

Leaves and sheaths generally glabrous with the lower sometimes slightly pubescent. Panicle open, sub-contracted or sub-secund, rarely secund. Spikelets rather large to medium, generally 2-flowered, sometimes or rarely 1-flowered, all aristate, or the upper only, very rarely muticate; glumes sub-unequal, shorter or sub-equal to the flowers, 7- to 9-nerved, 15 to 25 mm. long. Flowers all non-articulate and falling by fracture with the lowest flower generally stipitate; rachis more or less pilose or glabrescent; fracturing above and leaving the rachilla adherent to the basal flower; stipe of basal flower remaining between the glumes; lemma lanceolate, acuminate, generally glabrous on the back or rarely pilose to sub-pilose, apex passing into 2 awn points about 2 to 5 mm. long, exceeding or equalling the glumes; dorsal awn geniculate, very rarely reduced or absent.

Formerly cultivated in W. Europe and sub-spontaneous in many parts of Europe, especially the North.

Malzew differentiates the following types:

Var. 1. *Solida* (Hausskn). A rare form only known in N. Itica, Attica and Sinai.

sub-var. *tricholepis*, Holmberg. (= *A. strigosa* s.sp. *pilosa* var. *abba* = var. *fusca*, Marq.). Cultivated sparsely in Wales along with var. *glabrescente*.

Var. 2. *sub-pilosa*. Formerly and rarely cultivated with *glabrescente* in W. Europe.

sub. var. *orcadensis* (Marquand) Thell. This is the "small" oat of N. Scotland and the Shetland Isles.

Var. 3. *glabrescens* (Marquand) Thell. There are here five sub-varieties, all rare, including *sub-brevis*, cultivated or ruderal in N. Spain, W. France and Wales.

5a. *A. strigosa* s.sp. *strigosa* proles *brevis* (Roth) (Thell). (= *A. brevis*, Roth; *A. sativa* var. *brevis*, Körnicke, etc.) A 14-chromosome type which is now rarely found in cultivation, but occurs sub-spontaneously on sandy soils and as a weed in crops, mainly in the mountains of N. Lusitania and N. Spain, rarely in S.W. France (Pyrenees), Belgium (Ardennes), Wales and N.W. Germany.

The form is similar to s.sp. *strigosa*, but has the spikelets markedly shortened, generally 2-flowered; the glumes 7- to 8-nerved and 12 mm. long; the lemma oblong, obtuse, more or less stout, generally glabrous on the back, rarely pilose, the apex with 2 very short awn points (1 to 2 mm. long) and generally 1 (2) lateral tooth.

Three varietal forms are known.

5b. *A. strigosa* proles *nuda* (L) Hausskn. (= *A. nuda*, L. and *A. nudibrevis*, Vavilov.) A cultured form of N.W. Europe with 14 chromosomes, agreeing in many respects with s.sp. *strigosa*, and differing from other "nuda" types by the smallness of the caryopsis. This is the Piley corn or Pilcorn of early England.

Culms erect, rimy, with red nodes. Leaves and sheaths glabrous. Panicles sub-secund or almost contracted. Spikelets 3-flowered, with the flowers strongly

exceeding the glumes, the two lower flowers finely awned, the upper muticate ; inferior flower sub-sessile. Rachis strongly elongated and glabrous. Glumes sub-equal, shorter than the flowers, 7- to 9-nerved,  $\pm$  20 mm. long ; lemma lanceolate, becoming membranous with longitudinal nerves conspicuous, that of the lowermost flower with the apex divided and sub-aristulate. Caryopsis loosely enclosed in the membranous husks, short, about 6 mm. long by 1.5 mm. broad, more or less glabrous, the base rostellate and the apex shortly pappose.

6. *A. strigosa* s.sp. *abyssinica* (Hochst) Thell. (= *A. abyssinica*, Hochst.) A rarely cultivated type, generally found in cornfields. It has 28 chromosomes and has marked affinities with s.sp. *Vaviloviana*.

Distribution : Abyssinia, Eritrea (Jemen), Egypt.

Culm erect, leaves and sheaths glabrous, rarely with the lower pulverulent. Panicles open or very wide-spreading, frequently elongated and nodding ; spikelets mostly 2-flowered, rarely 3-flowered. Glumes sub-unequal, exceeding the flowers, 7- to 8-nerved, 20 to 25 mm. long ; flowers not articulate and disarticulating by fracture ; lower flower stipitate ; rachis more or less pilose ; inter-nodes of rachis fracturing above with the rachilla remaining attached to the inferior flower, whose stalk remains within the glumes ; lemma generally glabrous on the back, sometimes pilose, with 2 very short awn points ( $\pm$  1 mm. long), and 2 lateral tooth points. Dorsal awn geniculate or reduced.

Three varieties are described by Malzew.

#### SPECIES AND SUB-SPECIES OF SUB-SECTION : DENTICULATAE.

VI. *A. fatua* (L), Malzew. Non-cultivated, non-articulate. Culms erect or ascending, sometimes declining, sub-solitary or numerous, rounded, glabrous, smooth, about 5 mm. thick and about 1 m. tall ; nodes 3 to 4, glabrous or pubescent. Leaves, lanceolate, acuminate, wholly scabrous, green or glaucous, generally smooth and rimous at the base, about 28 to 30 cm. long and 8 to 10 broad, glabrous or ciliate at the margins, rarely pilose ; sheaths especially the lower pilose or glabrous ; ligule truncate, crenulate or denticulate, 3 to 5 mm. long, very rarely reduced. Panicle open, rarely sub-contracted or sub-secund, sometimes contracted or secund. Spikelets generally rather large, 2- to 3-flowered, sometimes several flowered, all or only the lower awned, rarely muticous ; glumes sub-equal, slightly exceeding or sometimes shorter than the flowers, 25 mm. (rarely 30 mm.) long, 9- to 11-nerved ; all flowers (rarely only the lower) articulate, falling, or rarely non-articulate and fracturing ; rachis of fertile and infertile flowers pilose or glabrous ; husks when mature coriaceous, fuscous, cinereous, flavous or white, rarely membranaceous, and straw-coloured or turning white ; lemma lanceolate or ovate-lanceolate, about 20 mm. long (rarely 25 mm.), strongly pilose towards the base, or slightly pilose or glabrous ; apex bidentate or shortly cleft and rough ; awn median dorsal ; base with callus or sub-sessile ; awns generally long, geniculate and twisted at the base, rarely slightly curved or straight, sometimes absent ; callus short obtuse, seto-pilose with a basal scar or none ; scar more or less oblique, ovate or sub-orbicular, margins elevated and bright ; pale shorter than and covered at the margins by the lemma, rarely uncovered, generally free at apex. Caryopsis 8 to 10 mm. long, corticate or rarely naked.



The following are the sub-species :

#### NON-CULTIVATED FORMS.

1. *A. fatua* s.sp. *meridionalis*, Malz. A sub-spontaneous form found in crops, chiefly in Buchara, Afghanistan, Turcomania, Persia, Transcaucasia, Asia Minor and extending into the Mediterranean region, especially in Egypt; introduced into N. America and Mexico. Chromosome number 48. Distinguished mainly by the great size of the spikelets.

Four varieties are distinguished.

2. *A. fatua* s.sp. *fatua* (L) Thell (= *A. fatua* L.). A very common sub-spontaneous form on corn lands, etc., throughout Europe, and elsewhere widely distributed. Chromosome-number 48. Culms sub-erect or ascending with the nodes always glabrous; leaves at the base ciliate on the margins; sheaths, especially the lower, pubescent; ligule 3 to 4 mm. long. Panicles about 30 mm. long, open, sub-contracted or sub-secund; spikelets rather large, 2- to 3-flowered, all awned; glumes slightly exceeding the flowers, 25 to 30 mm. long; all flowers (rarely only the inferior) articulate and readily falling; rachis below the inferior flower glabrous, at the base of others pilose, at the infertile flower pubescent; lemma lanceolate, about 20 mm. long, with a short obtuse callus bearing an ovate or sub-orbicular scar and seto-pilose; palea more or less covered by the lemma; grain fusiform, apex acute, about 17 to 20 mm. long by 2 mm. wide and 1.5 mm. thick. Caryopsis 8 mm. long, faintly sulcate, in cross-section obtusely triangular.

Four varieties are known.

3. *A. fatua* s.sp. *cultiformis*, Malz. A 48-chromosome subsegetal type, found especially in Canada and N. America, and also in Central and N. Europe and Central Russia, in association with s.sp. *praegravis*. Culms erect, nodes always glabrous. Leaves and sheaths glabrous; ligule 3 to 4 mm. long, very rarely absent; panicles 15 to 30 cm. long, polymorphous. Spikelets rather large, wide, 2- to 3-flowered, all flowers awned; glumes slightly exceeding the flowers, 17 to 25 mm. long; flowers all (occasionally only the lower) articulate and falling readily; rachis glabrous below, pilose at base of upper flowers, pilose on the stalk of the infertile flower; lemma ovate-lanceolate, 20 mm. long, with a short obtuse callus, the scar ovate to sub-orbulate, roughly pilose; awn geniculate, about 25 mm. long; pale generally enclosed at the margins by the lemma, generally free at the apex and rarely not enclosed at the margins. Husked grain sub-oval or oblong, thickened, often strongly convex on the back, and blunt at the tip, 17 to 19 mm. long, 2.5 to 3 mm. wide and 2.5 to 3 mm. thick, rarely shorter (14-15 × 2.5 × 2). Caryopsis 8 to 10 mm. long, barely sulcate, semi-rounded to rounded in section.

It also differs from all other sub-spontaneous s.sp. of *fatua* by the very short germination period.

Four varieties are known, divided into six sub-varieties.

4. *A. fatua* s.sp. *septentrionalis*, Malz. A sub-spontaneous or spontaneous weed form, growing in the mountains of Central Asia, especially the Pamirs, N. Russia, Siberia East and Central, Mongolia (probably China), and the mountains of Central Asia as far as the Pamir, Hindukush and N.W. Himalayas.

In habitat, sub-spontaneous or spontaneous. Culms erect or ascending, nodes always pubescent or rather villose. Margins of leaves ciliate rarely pilose; sheaths pilose. Panicles 15 to 30 cm. long, open, rarely sub-contracted, or sub-secund, sometimes almost contracted. Spikelets rather large, 2- to 3-flowered, all flowers awned; glumes slightly exceeding the flowers, 20 to 25 mm. long; flowers all articulate and later falling readily; rachis glabrous at the basal flowers, pilose above, with the stalks of the inferior flower pilose; lemma lanceolate, 20 mm. long, with a short obtuse callus and the scar ovate or sub-orbicular, seto-pilose; awn geniculate about 30 mm. long; pale more or less covered. Husked grain fusiform, with the apex acute, 17 to 20 mm. long, 2 mm. wide and 1.5 mm. thick. Caryopsis about 8 mm. long, with faint groove and obtusely triangular section.

There are four varieties.

#### CULTIVATED FORMS.

5. *A. fatua* s.sp. *macrantha*, Hackel. Rarely cultivated and generally occurring among crops in Persia, Transcaucasia, Asia Minor (probably passing into the Mediterranean area).

Allied to *meridionalis* but with all the flowers non-articulate and differing especially from other cultivated fatuas by the length of the spikelets. Nodes generally glabrous; glumes elongated up to 30 mm. long; spikelets large with all the flowers non-articulate; lemma elongate lanceolate, 20 to 25 mm. long; awn geniculate to slightly curved or straight, rarely absent; pale more or less open; husked grain fusiform, with the apex drawn out and acuminate, 25 mm. long, 2.5 mm. wide and 2 mm. thick.

There are four varieties.

5a. Proles *nudata*, Malz. A "nuda" form reported from Persia, and very close to *macrantha*.

6. *A. fatua* s.sp. *nodipilosa*, Malz. A cultivated form found especially in Russia and the Urals, Siberia and Mongolia. It is closely allied to *septentrionalis*, but all the flowers are non-articulate. Culms always pubescent at nodes (thus differing from other cultivated fatuas); glumes up to 25 mm. long; spikelets rather large, all flowers non-articulate; lemma lanceolate, 20 mm. long, husked grain fusiform with acute apex.

There are three varieties.

6a. Proles *decorticata*, Malz. Very closely allied to *nodipilosa*, but naked in habit. It is cultivated especially in the mountains of N. China and Mongolia.

7. *A. fatua* s.sp. *sativa* (L) Thell. (= *A. sativa*, L.). The most widely cultivated of all the oats, differentiated from s.sp. *fatua* mainly by the non-articulation of the flowers and from the cultivated s.sp. *nodipilosa* by the nodes being always glabrous. Culms erect or sub-erect, with the nodes always glabrous; leaves and sheaths glabrous; ligule very rarely absent; panicles open, sub-contracted or sub-secund, sometimes contracted or secund. Spikelets rather large, 2- to 3-flowered and rarely 1-flowered, the lower flowers only awned, rarely all muticate. Glumes up to 25 mm. long, slightly exceeding the flowers; all flowers non-articulate and separating by fracture; area of fracture rudimentary, indistinct and sub-horizontal; rachis glabrous or slightly glabrous; inter-node

of rachis fracturing above with the rachilla remaining attached to the lower flower, sometimes fracturing somewhat below, leaving the rachilla attached to the base of the upper flower; lemma lanceolate, about 20 mm. long, sub-sessile, generally glabrous, surrounded at the base by a few hairs or totally glabrous; awn geniculate or slightly curved or almost straight or absent; palea more or less covered; husked grain fusiform with an acute apex, about 20 mm. long, 2 mm. wide by 1.5 to 2 mm. thick.

The following forms are described by Malzew :-

- Var. 1. *Pilosa*, Koeler. Rare.  
     Sub-var. *sub-pilosa*, Thell.  
     Sub-var. *glabricula*, Thell.
- Var. 2. *Sub-uniflora*, Trabut. Frequent.
- Var. 3. *Brachytricha*, Thell. Often common.  
     Sub-var. *spelticosa*, Malz.  
     Sub-var. *pseudo-transiens*, Thell.
- Var. 4. *Glaberrima*, Thell (= *A. sativa*, L., in the strict sense). This includes a very large number of the cultivated forms.  
     Sub-var. *contracta*, Neilreich (= *A. orientalis*, Schreber, and *A. sativa orientalis*, Alefeld).  
     Differing by the second panicle : common.\*  
     Sub-var. *eligulata* (Vavilov). Contracted and without a ligule.

7a. *Proles chinensis*, Fisch (= *A. chinensis*, Metzger; *A. sativa*, var. *chinensis*, Noell).

Culms erect or sub-erect with the nodes always glabrous; leaves and sheaths glabrous; panicles open, rarely secund, spikelets 3-flowered, the flowers standing out beyond the spreading glumes, with the lower awned or muticate; glumes up to 25 mm. long, shorter than the flowers; lemma lanceolate, up to 20 mm. long, frequently membranous with the longitudinal nerves conspicuous; caryopsis naked, loosely enclosed by the husk, about 8 mm. long by 2 to 2.5 mm. thick, glabrous with the apex shortly pappose.

8. *A. fatua* s.sp. *praegravis*, Krause (= *A. sativa praegravis*, Krause). A cultivated form closely resembling s.sp. *cultiforme*, but with all the flowers non-articulate. It can be differentiated from the other cultivated forms by the ovate-lanceolate lemma (about 20 cm. long) and the somewhat open pale. The husked grain is sub-oval or oblong, thickened and generally strongly convex on the back with the apex obtuse, about 14 to 20 mm. long, 2 to 3 mm. wide and 2 to 3 mm. thick.

Cultivated chiefly in Central Russia, Central and North Europe, Canada and N. America. Malzew described four varieties of which var. *leiantha*, Malz., is the commonest.

8a. *Proles grandiuscula*, Malz. (= *A. sativa* var. 25, *inermis*, Körnicke and *A. sativa* var. 26, *chinensis*, Körnicke). Cultivated in Europe, Canada and N. America.

Similar to s.sp. *praegravis*, but with the flowers exceeding the glumes, which are often membranous and strongly veined; caryopsis naked. A very rare secund form is known.

VII. *Avena sterilis* (L) Malzew. Culms prostrate, then ascending from the base, declining or sub-erect, at times caespitose, sub-solitary or many, rounded, glabrous, smooth, generally about 5 mm. in diameter and about 1 m. in height; with 3 to 4 nodes, glabrous or rarely pubescent. Leaves lanceolate-acuminate, generally scabrous, glaucous or green; often smooth but rimy, mostly about 25 to 30 cm. long and 10 mm. wide; glabrous or ciliate at the margins; ligule truncate and cut, 4 to 6 mm. long; panicle sub-secund, nodding or open, often sub-contracted, very rarely secund. Spikelets generally very large or large, rarely rather large or small, 2- to 5-flowered, the two lower flowers kneed, often seto-pilose, the remainder glabrous. Glumes sub-equal, exceeding the flowers, sometimes shorter, about 25 to 50 mm. long, 9- to 11-nerved; the lower flower only articulate and later readily falling, the upper non-articulate and separating by fracture; rarely with all the flowers non-articulate; rachis wholly glabrous; husk coriaceous, fuscous or cinereous or flavous, rarely straw-coloured and membranous; lemma of inferior flower lanceolate, about 20 to 40 mm. long, seldom pilose or sparsely pilose from base to middle, or glabrous with apex bidentate or very rarely bisubulate and scabrous; callus basal or sub-sessile; awn medium and dorsal, generally very long, strongly geniculate and twisted below, rarely slightly curved and not twisted; callus short, obtuse, broad, seto-pilose, with a basal scar or rarely a very indistinct one; scar oblique, oblong or oval, sometimes orbicular oval, with the margins rough and shining; palea short, exposed almost to the middle; caryopsis 9 to 12 mm. long, usually husked but very rarely naked.

The following are the sub-species.

#### NON-CULTIVATED FORMS.

1. *A. sterilis* s.sp. *trichophylla*, C. Koch. Em. Hausskn. A spontaneous to sub-spontaneous form found on dry hills and mountain-sides in Asia Minor, Syria, Palestine, Mesopotamia, W. Persia, Transcaucasia and Tauria; introduced into the W. Mediterranean region.

It is more or less intermediate between s.sp. *Ludoviciana* and s.sp. *macrocarpum*, differing chiefly by the pubescence of the nodes. Malzew distinguishes two varieties.

2. *A. sterilis* s.sp. *macrocarpa* (Monch), Briq. (= *A. sterilis* L. *sensu stricto*: *A. sterilis* s.sp. *macrocarpa*, Briq.). A spontaneous to sub-spontaneous form distinguished by its large spikelets. Found in the Mediterranean region of Europe and N. Africa from the Canaries to Maritime Anatolian, the littoral of Syria, Palestine, Arabia, Abyssinia and Egypt, introduced into Central Europe, S. Africa and parts of S. America.

Four varieties are known.

3. *A. sterilis* s.sp. *Ludoviciana*, Dur. (Gillet et Magne). (= *A. sterilis* s.sp. *Ludoviciana*, Gillet et Magne; *A. Ludoviciana*, Dur.) A spontaneous to sub-spontaneous form extending from Turkestan and Afghanistan through S. Turcomania and Persia, S. Russia, Tauria and Asia Minor, becoming rare in the West, found especially in the Mediterranean region sub-spontaneously. Often very abundant in grain fields.

S.sp. *Ludoviciana* differs chiefly from s.sp. *macrocarpa* by the smaller

spikelets which are 2-, rarely 3-flowered ; the shorter glumes (about 25 mm. long) and the shorter lemma of the lower flower.

It has frequently been confused with *A. fatua*, L., from which it differs by the fact that only the lower flower is articulate whilst the upper are non-articulate and that the scar is oblong or oval and never ovate or sub-orbicular.

Var. *typica* with seven sub-varieties and three others are known.

#### CULTIVATED FORMS.

4. *A. sterilis* s.sp. *nodi-pubescens*, Malz. This form is either cultivated or sub-segetal in Asia Minor as far as Palestine. It is closely related to s.sp. *trichophylla*, but all the flowers are non-articulate. It differs from all other cultivated s.sp. of *sterilis* by the pubescent nodes.

5. *A. sterilis* s.sp. *Byzantina* (C. Koch) Thell. (= *A. sterilis* s.sp. *Byzantina*, Thell ; *A. Byzantina*, C. Koch ; *A. Algeriensis*, Trabut ; *A. sterilis* s.sp. *culta* Marq.) Cultivated in the whole of the Mediterranean region, introduced into America and S. Africa. Closely allied to s.sp. *macrocarpa*, from which it differs by the flowers being all non-articulate.

Cultivated or sub-segetal, mid-season or late. Culms prostrate, becoming ascendant or sub-erect, with glabrous nodes. Panicles open, contracted or sub-second, very rarely secund ; spikelets large, 3- to 4-flowered, the two lower, rarely only the lowest, awned ; glumes exceeding the flowers,  $\pm$  30 mm. long ; all flowers non-articulate and fracturing, the small scar of the lower flower rather wide, strongly oblique ( $45^\circ$ ), slightly concave or flat, very rarely rudimentary ; rachis fracturing below and leaving the rachilla attached to the base of the upper flower ; lemma of lower flower  $\pm$  25 mm., sub-sessile, generally glabrous on the back and with a few hairs at the base ; awns slightly curved, not twisted, rarely geniculate and more or less twisted ; caryopsis about 11 mm. long.

The following varieties are known :

Var. 1. *Solida*, Hausskn., very rare.

Sub-var. *segetalis*, Bianca, very rare.

Sub-var. *secunda*, Malz., secund.

Sub-var. *induta*, Thell., rare.

Var. 2. *Macrotricha*, Malz. Lemma glabrous on back with long hairs (5 mm.) at base.

Sub-var. *pseudo-vilis*, Hausskn. Lemma coriaceous, the lower flower tending to fall.

Sub-var. *hypo-melanthera*, Thell.

Sub-var. *biaristata* (Hackel) Thell., in Algeria especially. Awn only slightly curved and the glumes strongly exceeding the flowers.

Sub-var. *culta*, Thell. Awns shorter than in *biaristata*, with only the awn of the lowest flower exceeding the glumes, of the second muticous ; very common.

Sub-var. *solidissima*, Thell. Basal flower strongly solidified.

Var. 3. *Brachytricha*, Thell. Basal hairs very short, very rare.

Var. 4. *Hypotricha*, Thell. Probably introduced into Switzerland.

5a. Proles *denudata*, Hausskn. A "naked" form allied to *byzantina*.

6. *A. sterilis*, ss. *pseudo-sativa*, Thell. A rare form. Cultivated or sub-segetal. Culms erect or sub-erect with glabrous nodes. Leaves and sheaths glabrous; panicle elongated open and much branched. Spikelets rather large, 2-flowered, both flowers, rarely the lower awned; glumes  $\pm 25$  mm., exceeding the flowers; all flowers non-articulate and separating by fracture, the point of attachment of the lower flower strongly oblique ( $45^\circ$ ), and slightly concave, very rarely rudimentary; rachis fracturing below, leaving the rachilla attached to the base of the upper flower; lemma of first flower 20 mm. sub-sessile; awn geniculate, slightly twisted or slightly curved and non-twisted; caryopsis about 8 to 9 mm. long. Distribution: Switzerland and also Uruguay.

As already noted, the above classification is in conformity with the chromosome numbers. In the section Aristulatae, both the *Inaequaliglumis* and the *Stipitatae* have  $7/14$  chromosomes. In the section Denticulatae, the single species *A. strigosa* s. *ampl.* is divisible into two karyological types, the one branch having  $7/14$  chromosomes and exhibiting affinities with the other members of the  $7/14$  group, the second branch possessing  $14/28$  chromosomes and forming a definite group by themselves. Finally, the section Denticulatae represented by the members of the species, *A. fatua* s. *ampl.* and *A. sterilis* s. *ampl.* have  $21/42$  chromosomes and again constitute a more or less compact group.

Inter-specific hybridization studies indicate the relative apartness of the members of the three groups. Thus Malzew states that it is not possible to cross the species of sub-section Aristulatae with those of sub-section Denticulatae; and that *A. strigosa* s.sp. *barbata* ( $2x = 28$ ), is very difficult to cross with *A. strigosa* s.sp. *strigosa* ( $2x = 14$ ). On the other hand, inter-crossing between members of the same chromosome group are readily obtained. These claims, however, cannot be substantiated. Triploid, Tetraploid and Pentaploid hybrids have been secured (see pages 72-78) though it is true that many are only obtained with difficulty.

The immunity studies of Vavilov, Reed and others also tend to support the naturalness of the classification. Broadly speaking the species of sub-section Aristulatae are more immune to disease than those of sub-section Denticulatae. The serological studies of Zade also indicate that *A. sativa*, L. and *A. fatua* L., are closely related whilst *A. byzantina* and *A. strigosa* differ from both and from one another. Finally the geographical distribution is in general conformity with the grouping.

The inter-relationships of the species is shown in Tables IX and X.

FATUOID OATS.—Zade (1918) states that the first description of fatuoid oats was made by Haussknecht in 1884. He was of the opinion that they were transitional forms between the wild-oat *A. fatua*, L., and *A. sativa*, L., and accordingly named them "Zwischenformer" or *A. fatua* var. *transiens*. Since then a large number of such types have been discovered, not only in varieties of *A. sativa*, but also in varieties of *A. Byzantina*, usually regarded as the cultivated derivatives of *A. sterilis*. Stanton, Coffman and Wiebe have given a detailed list of the types discovered up to 1926. A considerable number of accessions could now be added to their list.

In addition to "true" fatuoids, somewhat similar types exist which appear

to be due to natural crossing between *A. fatua* and *A. sativa*. Such forms are in general intermediates, and on selfing give rise to a complex series of segregates involving a number of characters.

True fatuoids, on the other hand, appear to be derivatives of *A. sativa*, *A. Byzantina*, or allied cultivated types which resemble the variety in which they occur in many respects but also differ in the possession of a series of characters which have been termed the "fatuoid complex." The most striking features of this complex consist of :—

1. The presence of a distinct articulation or cavity ("suckermouth") at the base of the grain.
2. Long dense hairs or bristles surrounding the cavity.
3. Similar hairs on the attached rachilla.
4. A twisted geniculate awn on all the lemmas of a spikelet.
5. A tendency to shatter at maturity.

Forms which possess these associated characters in general breed true and have been referred to as "homozygous" fatuoids by most investigators. The name *A. sativa* mut. *fatuoida*, has also been suggested as appropriate by Huskins and Fryer (1925).

The intermediate forms in which semi-abscission is found together with a less prominent cavity, reduction in the basal hairs and a tendency towards floret disjunction by disarticulation, constitute the group of heterozygous fatuoids. (Fig. 7 (C).) According to Huskins (1927), these heterozygous forms are in general the first to appear, but Marquand (1922) discovered the direct appearance of a homozygous form from one seed of the variety Victory (*A. sativa*).

Normally, heterozygous fatuoids segregate into homozygous fatuoids and normal types in the proportion of 1 : 2 : 1. Divergent ratios, however, have been found, and certain of these types have been studied cytologically.

More recently, Stanton, Coffman and Wiebe (1926) reported the occurrence in varieties of *A. Byzantina*, of fatuoids with all the characters of the "fatuoid complex" fully developed, which nevertheless breed true. They accordingly suggest a modification of the above terminology, viz. :—

1. Homozygous fatuoids for the true breeding types.
2. Heterozygous fatuoids for those phenotypically resembling the homozygous forms, but genotypically unlike, and exhibiting segregation.
3. "Heterozygous cultivated" for the intermediate segregating forms (=heterozygous fatuoids of most investigators).
4. "Homozygous cultivated" for the normal.

Huskins (1927), however, is of the opinion that the above "heterozygous fatuoids" which do not breed true may be the result of natural crossing, and therefore considers that the term heterozygous fatuoids for intermediates should be retained until more is known about the types in question.

Three opinions as to the origin of fatuoids have been advanced :—1. natural crossing ; 2. chromosome aberration ; 3. gene mutation. They will be considered in that order though the chromosome aberration hypothesis is more recent than the gene mutation hypothesis.

I. NATURAL CROSSING HYPOTHESIS.—Körnecke and Werner (1885) attributed the origin of what appeared to be fatuoids to natural crossing. This hypothesis was supported by Zade (1912-1918), who discussed his investigations in his book *Die Hafer* (1918).

Zade stated that grains exhibiting characters intermediate between *A. sativa*, brown or yellow in colour, are of frequent occurrence in samples of cultivated oats. These intermediates segregated into 1 *sativa* : 2 intermediates : 1 *fatua*. His description of these segregates indicate that they were similar to those now spoken of as normal cultivated, heterozygous fatuoid and homozygous fatuoid respectively. Since they resembled the segregates obtained from the F<sub>1</sub> of the cross *sativa* × *fatua*, he came to the conclusion that they were segregates, heterozygous for one factor, from natural crosses of *sativa* and *fatua* which had taken place several years previously. In support of this contention, he pointed out that the intermediates found in cultivated samples were too numerous to be due to mutation and that examination of many samples indicated a positive correlation between the number of intermediate type grains and the number of wild type grains present.

Tschermak (1929) obtained F<sub>1</sub> plants from several crosses between *A. sativa* and *A. fatua*, which corresponded, except in the case of lemma pubescence, to the description of heterozygous fatuoids. In the F<sub>2</sub> generation, three types of segregates, *fatua*, intermediate and *sativa*, were obtained in a ratio of 4 : 9 : 3. A tri-factorial hypothesis was devised to explain the situation.

Aamodt, Johnson and Manson (1934) studied the progeny of a cross between *A. fatua* (with oblique "suckermouth" articulation, heavy pubescence on rachilla, callus and lemma, dark brown or black lemma, and strong geniculate awns on all grains of the spikelet)—and *A. sativa* (selection 76, with non-oblique articulation and no "suckermouth," sparse pubescence on callus and rachilla (or glabrous), lemma glabrous and white and all grains awnless). In the F<sub>1</sub> generation, the black lemma colour tended to be dominant; the awn varied from weak to strong on the primary grain, but was absent on the secondary; rachilla pubescence varied from complete absence to the intermediate condition; callus pubescence varied from sparse to medium, dense tufts of short to medium hairs on the first grain with no expression on the second; lemma pubescence was found on the first grain as sparse, short to medium scattered hairs, with no hairs on the second grain; the articulation was intermediate—there was no "suckermouth," but the abscission surface was larger than in *sativa* and tended to be oblique as in *fatua*. (Fig. 7.)

In the F<sub>2</sub> generation, all combinations of lemma colour, awn development and pubescence were found. As regards articulation, three more or less definite types occurred, *fatua*, intermediate and *sativa*. There was also close linkage between articulation, awn development, rachilla and callus pubescence—the so-called "fatuoid complex."

On the basis of the segregation obtained, Aamodt and his co-workers postulated the following factors :—

*B*, an epistatic factor for black lemmas.

*G*, a factor for grey colour, epistatic to *b* or *g* or both, but hypostatic to *B*.



*W*, a gene complex controlling awn development, articulation and rachilla and callus pubescence; *WW* produces fatua; *Ww* intermediate and *ww* sativa type.

The F<sub>2</sub> progeny obtained could, therefore, be classified as consisting of the following phenotypes :—

Phenotype.		F <sub>2</sub> frequencies.	
		Observed.	Calculated.
Black Wild	<i>BW</i>	14	12.94
Black Intermediate	<i>BI</i>	21	25.87
Black Cultivated	<i>Bw</i>	19	12.94
Grey Wild	<i>GW</i>	1	3.23
Grey Intermediate	<i>GI</i>	4	6.47
Grey Cultivated	<i>Gw</i>	6	3.23
White Wild	<i>bW</i>	1	1.08
White Intermediate	<i>bI</i>	3	2.16
White cultivated	<i>bw</i>	0	1.08

Three homozygous fatuoid types (*bI*) and one homozygous fatuoid type (*bW*) were accordingly obtained, thus affording "definite proof that these types can originate as a result of hybridization between *A. fatua* and *A. sativa*." Since they also appeared in the F<sub>3</sub> generation from such F<sub>2</sub> plants as *BbWw* and *BbWW*, the proof was regarded as "rather conclusive." "In morphological characteristics and in breeding behaviour these 'synthetic' fatuoid types correspond exactly to the common fatuoid. . . ."

Aamodt *et al.*, having shown that natural crossing between *fatua* and *sativa* may take place, then studied the progeny from aberrant forms found in the field and believed to have originated as crosses between *fatua* and *sativa*. Some of the types were found to be homozygous, others heterozygous. The heterozygous forms segregated in a manner which paralleled that of the artificial hybrids, and extracted fatuoid types were again obtained. Thus from a black aberrant of the *BI* type, there were obtained 9 black wild (*BW*), 3 homozygous fatuoids (*bW*) and 4 heterozygous fatuoids (*bI*): from a grey aberrant of the *GI* type, five of the plants were grey wilds (*GW*), two were typical homozygous fatuoids (*bW*), and four were typical heterozygous fatuoids (*bI*).

Aamodt and his co-workers are, therefore, convinced that fatuoids of the *A* type may and do originate through natural crossing, not as immediate segregates but as later segregates from a cross which occurred several years before.

There remains, however, the difficulty that fatuoids in the field are not invariably associated with large numbers of black and grey aberrant forms, which should be the case if they are segregates from natural crosses. According to Aamodt this is due to the fact that the non-fatuoid aberrant types are readily eliminated. "Our observations in the field, and in the seed cleaning plants, have shown that the selective elimination of all phenotypes except the three types mentioned above (*i.e.*, normal, heterozygous and homozygous fatuoid) is exactly what one would expect to take place, following hybridization of *A. fatua* with *A. sativa* in cultivated oat fields in which selection is practised." Where selection does not take place the other aberrant forms must occur, and according to the evidence of field inspectors (in Canada), do occur.

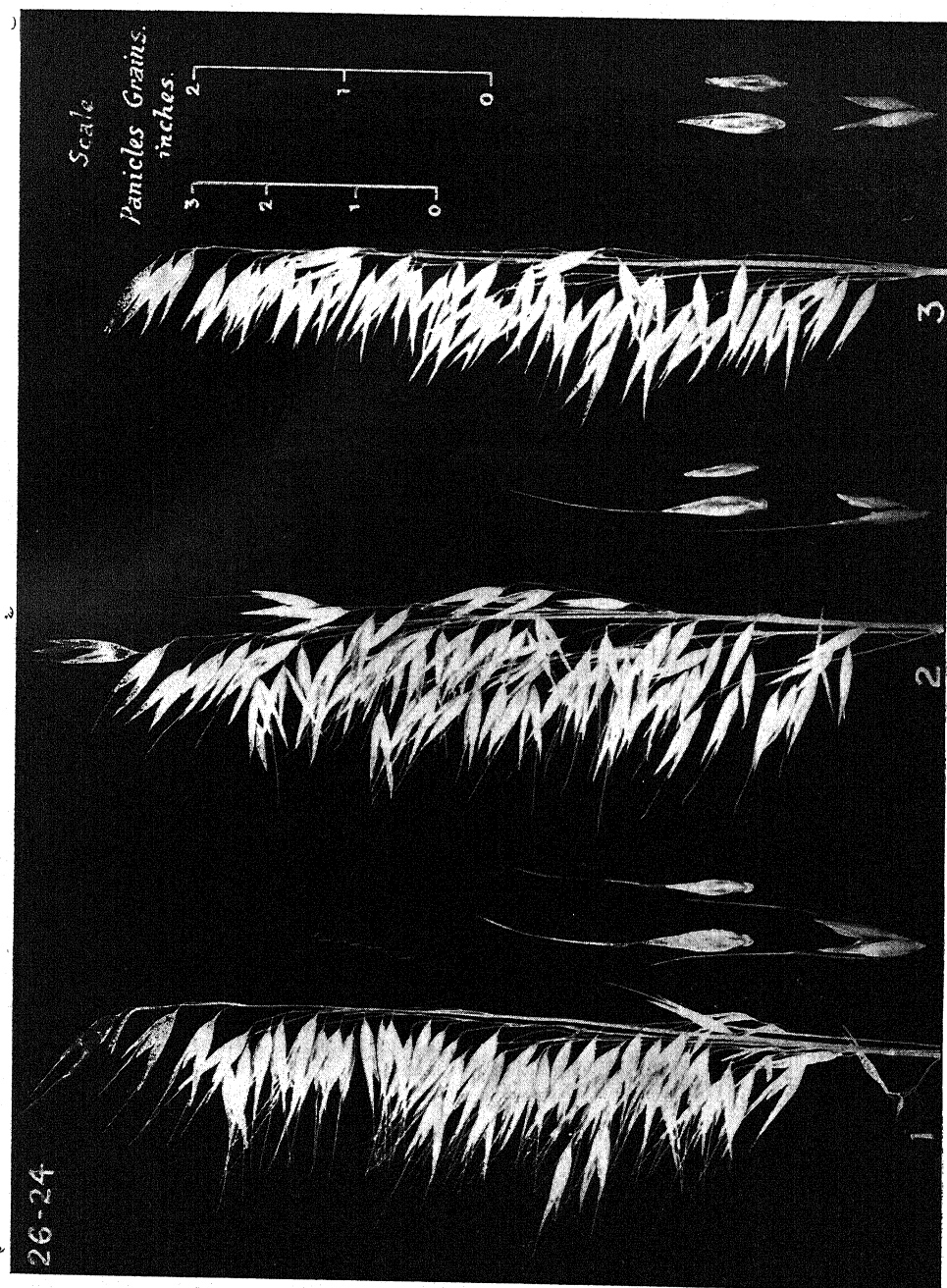


FIG. 19.

1, 2 and 3. Homozygous fatuoid, heterozygous fatuoid and normal type segregates all with 42 chromosomes, derived from a heterozygous fatuoid  $F_1$  out of the cross homozygous fatuoid Sir Douglas Haigh X normal Sir Douglas Haigh. Enlarged Figures: lower—a spikelet with outer glumes removed; upper—a similar spikelet with florets separated. (After Huskins.)

The above evidence indicates that A type fatuoids may be obtained as ultimate segregates from the cross of *A. fatua*  $\times$  *A. sativa*.

2. CHROMOSOME ABERRATION HYPOTHESIS.—Stanton, Coffman and Wiebe (1926), in a study of fatuoids derived from Byzantina varieties, came to the conclusion that chromosome irregularity might offer a satisfactory explanation of their origin. Goulden (1926) and Huskins (1927) found a number of fatuoid types which did not segregate in a 1 : 2 : 1 ratio, and pointed out their analogy to the speltoid series found in *Triticum* (see page 183). Huskins (1925, 1927, a. and b.) further studied a number of types cytologically and divided them into three series, corresponding to the speltoid series.

a. *Fatuoids of the A-series*.—The commonest type of heterozygous fatuoid segregates into homozygous fatuoids, heterozygous fatuoids and normals in a 1 : 2 : 1 ratio. Huskins (1927) found that all these segregates and the original heterozygous forms had the normal chromosome number of 42. At diakinesis and at the heterotypic metaphase of the pollen mother cells, all normal segregates had  $21''$  chromosomes: heterozygous fatuoids had frequently  $19'' + 1''' + 1'$ : homozygous fatuoids had  $19'' + 1''''$ . He concludes "that an occasional aberration (probably the formation of a quadrivalent) in the meiotic division of normal cultivated oats produces a gamete in which one particular chromosome bearing fatua or fatuoid characters is duplicated and another bearing normal type factors is absent." In the normal, the sativa characters would be epistatic to the fatua characters. In the heterozygote there would therefore be 3 fatua chromosomes to 1 sativa, and the balance would accordingly be upset. Segregation of the chromosomes of such a heterozygous form would give a 1 : 2 : 1 ratio. (Fig. 19.)

b. *Fatuoids of the B-series*.—A second type (Type 2) of fatuoid exhibited complex segregation. Huskins found that it possessed 41 chromosomes, regularly arranged as  $20'' + 1'$ . A third type (derived from one of the above) gave rise to heterozygous fatuoids and normals in the ratio of 4 : 1 plus a few sterile dwarf homozygous fatuoids. They were found to contain 40 chromosomes with completely irregular meiotic divisions.

c. *Fatuoids of the C-series*.—A fourth and rare type gave evidence of segregating in a 1 : 2 : 1 ratio. The heterozygous forms were found to contain 43 chromosomes arranged either as  $20'' + 1''' + 1'$  or  $21'' + 1'$ . The homozygous segregates were dwarf and sterile. All had 44 chromosomes, arranged either as  $22''$  or  $20'' + 1''''$ .

On the basis of Winge's hypothesis (see page 184), Huskins (1927a) first suggested that normal sativa forms could be represented by the formula  $\frac{S_1 S_2 F}{S_1 S_2 F}$ , if two species were represented in their ancestry; by  $\frac{XSF}{XSF}$ , if three species were represented.

Later (1927 b) he adopted the simpler formula  $\frac{ABC}{ABC}$ , where B represents the chromosome carrying the fatua factors and C the chromosome carrying the sativa factors. The formulae for the heterozygous fatuoids would accordingly be:—

For the A-series,  $\frac{ABC}{ABB}$  ;  
 For the B-series,  $\frac{ABC}{ABO}$  ;  
 For the C-series,  $\frac{ABC}{ABCB}$  .

In the A-series, therefore, the appearance of the fatuoid would be due to the presence of an extra B, pairing with C or forming a trivalent with the normal B-pair ; in the B-series the absence of a C-chromosome would unmask the fatuoid factors present in the B-chromosomes ; in the C-series, the presence of an additional B-chromosome would again upset the "balance" and permit the expression of the fatuoid characters.

Ivanoff (1930) found evidence of multiple allelomorphs involving specific character complexes in *sativa*, *sterilis* and *fatua* types, the latter being dominant. He believes that the fatuoids are quite distinct from *A. fatua*, and that they are due to chromosome aberration.

These conclusions have since been modified in relation to more recent findings. As Huskins himself has expressed it : "instead of duplication of whole chromosomes, it is now clear that only parts are duplicated in some mutants." This adjustment is based on the following evidence.

In series B fatuoids, segregations of about 5 : 1 are common ; segregations of 10 : 1 and even 20 : 1 may also occur. Also, in all the series the homozygous form is rare. When present it is dwarf and sterile, possessing 40 chromosomes. The sterility is due to the fact that all 40-chromosome forms are asynaptic. It follows, therefore, that the C-chromosomes must be carrying genes for normal pairing and cell division : if both sets are absent, asynapsis must occur : if one set be absent (*i.e.*, one C-chromosome missing), then the effect is less drastic though variable.

The position in the B-series fatuoids is accordingly more or less as before. The C-chromosome carries genes for the *sativa* characters plus genes for normal pairing division. If one be absent, the heterozygous fatuoid type emerges. At meiosis, gametes with either 20 or 21 chromosomes form. In different strains, the frequency with which the unpaired chromosome is lost varies. The ratio of 41 : 42 chromosome progeny (*i.e.*, of normal to heterozygous plants) is practically the same as the ratio of 20 and 21 chromosome gametes. On the female side, both 20 and 21 gametes function normally : on the male seed, fertilization by 20 chromosome gametes is rare. Occasionally, however, a 20-chromosome pollen grain will mate with a 20-chromosome egg. The result is a dwarf, asynaptic and, therefore, sterile homozygote.

In C-series fatuoids, certain of the strains undoubtedly possess 43 chromosomes in the heterozygous forms, 44 in the homozygotes and 42 in the normal. Segregation of the heterozygotes give approximately 1 : 1 ratios, with few almost sterile homozygotes. Here the presence of an extra B chromosome seems to meet the situation. Evidence has now been obtained, however, that certain C strains, instead of having an extra chromosome, have lost part of the C chromosome. (Nishiyama, 1933, a and b ; Huskins, 1933.) Critical examination of the C chromosome showed that its long arm ( $S_1$ ) contributed to normal pairing, whilst

its short arm ( $S_2$ ) contributed to the development of the cultivated characters (*sativa*). In these strains, therefore, the short arm ( $S_2$ ) of the C chromosome has apparently been lost, the deletion carrying with it the genes for the *Sativa* complex. But the long arm is retained and, as a consequence, the factors for normal pairing are still operative.

In the A-series fatuoids, the genetic tests have shown that Huskin's original conception that a C chromosome was missing and a B chromosome substituted, cannot be accepted. (Nishiyama, 1931; 1933, a and b; Jones, 1930.) The original conception was based on the assumption that occasionally a C chromosome would mate with a B. But chromosome pairing is now being regarded as a function not of whole chromosomes but of unit parts. (See Darlington, 1932.) Hence, irregular pairing of a B and C chromosome could result in an exchange of segments, resulting in the formation of a chromosome, in which part of the B has been deleted and part of a C substituted (and conversely). A plant ABC with a chromosome Bc could, therefore, express fatuoid characters, and further, would tend to exhibit a trivalent at meiosis. In the series-A strains which approach the C-series in genetic types, a pair of very slightly unequal chromosomes occur, evidently due to the loss of a small part of one of the C chromosomes.

3. THE GENE-MUTATION HYPOTHESIS.—Evidence in support of the origin of fatuoids by mutation has been advanced by Howes (1908); Thellung (1911); Criddle (1912); Nilsson-Ehle (1911, 1921 a); Newman (1912, 1923); Akerman (1921); Gante (1921); Marquand (1922); Garber (1922); Garber and Quisenberry (1923) and Parker (1924). Its chief support, however, is to be found in the work of Nilsson-Ehle. More recently, Jones (1930 and 1932) and Nishiyama (1930) have supplemented this hypothesis.

Jones (1930 and 1932) obtained fatuoids not only of the normal A-series, but a number of aberrant forms which differed in certain respects from the A-series, but nevertheless had 42 chromosomes. The more important of these were strongly awned types, showing a tendency to partial solidification of the base (ex. *sativa* and *Byzantina* varieties); weakly awned types (chiefly ex *Byzantina* varieties); a sub-fatuoid from an F<sub>4</sub> family ex Red Algerian × Golden Rain; a fatuoid mutant from Golden Rain differing in spikelet number as well as in grain form from the mother plant.

Genetical studies of all these forms indicated that the characters of each were associated in inheritance and that there was a simple allelomorphic relationship between the expressions. All had 42 chromosomes and the segregates were of equal vigour.

Such a situation, it is argued, does not appear to be compatible with the occurrence of chromosome irregularity, but is explicable on a basis of gene-mutation. Thus if the formula  $\frac{ABC}{ABC}$  be taken to represent the di-triploid chromo-

some group whose inter-actions are concerned with the development of the fatuoid characters, the situation could be envisaged in the following manner. Let the B chromosome carry the factors (amongst others) for the fatuoid complex and for low spikelet number; let the C chromosome carry the factors for the *sativa* complex and for high spikelet number; assume further that the C factors

are epistatic to the B factors. Then in a normal type  $\frac{ABC}{ABC}$ , the sativa complex of the C chromosomes would mask the presence of the fatua complex in B, and as a consequence the grain characters would be non-fatuid in expression—i.e., they would be sativa in character. Here it should be noted that the factors postulated on B are not merely the fatua counter-part of the sativa factors on C, but "fatua" factors plus others; the same is true of the factors on C. Should, however, a factor mutation occur in C, such a mutation could un-mask its hypostatic counter-part in B. "The extent to which factors borne by B would find expression, would depend upon the nature and extent of the mutation occurring in C." (Jones, 1930.) Thus a mutation  $C_1$  could give rise to one expression and mutation  $C_2$  to a second and different expression; a mutation  $C_3$  to a third expression, etc.

On this basis, Jones (1930) has put forward the following formulae, in order of increasing complexity, for the more important sativa fatuoids in the heterozygous condition.

For the strong awned type A,  $\frac{ABC}{ABC_1}$ .

For the A-series fatuoids,  $\frac{ABC}{ABC_2}$ .

For the Golden Rain fatuoids,  $\frac{ABC}{ABC_3}$ .

For B-series fatuoids,  $\frac{ABC}{ABO}$ .

For C-series fatuoids,  $\frac{ABC}{ABBC}$  or  $\frac{ABC}{ABC_2C}$ .

The above formulae for all 42-chromosome types would permit simple segregation with the normal: each mutant  $C_1$ ,  $C_2$ ,  $C_3$ , would behave as a simple allelomorph to the other, and give accordingly simple segregation when intercrossed with one another. The formula for the B and C series, showing uneven chromosome numbers, would permit only of ratios in the segregates corresponding to those actually obtained.

Since Jones (l.c.) is of the opinion that the third or C chromosome in *sativa* cannot be identical with the third chromosome of *Byzantina* forms (= *sterilis culta* forms), he uses the formula  $\frac{ABD}{ABD}$  for this species.

The corresponding formula for the chief fatuoids of this species would then read:

For Type A,  $\frac{ABD}{ABD_1}$ .

For weakly awned types,  $\frac{ABD}{ABD_2}$ .

For Type B,  $\frac{ABD}{ABD_3}$ .

For sub-fatuid,  $\frac{ABD}{ABD_4}$ .

For the A-series from Fulghum,  $\frac{ABD}{ABD_5}$

For B-series fatuoids,  $\frac{ABD}{ABO}$

For C-series fatuoids,  $\frac{ABD}{ABBD}$  or  $\frac{ABD}{ABD_5D}$

On this hypothesis accordingly there is no necessity whatsoever to postulate the occasional pairing of B with C.

Nishiyama (1930, 1931) in a cytological study of fatuoids, found meiotic irregularities in the A-series of fatuoids but concluded that these irregularities need not necessarily be the result of the fatuoid constitution. The mutation in the C-chromosome he considered to be the likely explanation of the origin of the A-series. In a later paper (1933), Nishiyama again argues against the chromosome aberration hypothesis for the A-series of fatuoids. He found no mating of the B- and C-chromosomes, thus ruling out the formula  $\frac{ABC}{ABB}$ ; no synapsis occurred in

the absence of C, rendering the formula  $\frac{ABB}{ABB}$  untenable. He considers that the evidence so far obtained indicates linkage of the sativa characters but not necessarily of the fatua characters; and that the fatua characters are hypostatic and probably on a different chromosome. His later opinion on the nature of the A-series has already been discussed.

Coffman and Taylor (1932) found that fatuoids appeared suddenly in selfed Fulghum oats in 0.2 per cent. of the plants. They first appeared as heterozygotes and are regarded by these authors as mutations.

Jones (1932) in studying the progeny of a cross between *A. barbata* ( $2n = 28$ ) and *A. brevis* ( $2n = 14$ ), obtained diploid segregates in which equivalents of the "fatuid complex"—basal articulation, basal pubescence and strong awn—was broken down. This is regarded as an instance of crossing-over within the complex. Jones accordingly is of the opinion that the appearance of these exceptional "cross-overs" must in this instance have been due to "chromosome aberration," i.e., to the exceptional pairing of a B with a C chromosome which in his opinion would permit "crossing-over" to take place. As this is the only instance known of the breakdown of the "fatua" complex (i.e., of crossing-over between the factors of the complex) it follows that fatuoids cannot normally be due to "chromosome aberration." On the other hand, if B normally mates with B and C with C (and complex gene mutation takes place in C of such a nature as to permit the expression of the "fatua" complex latent in B) then no "cross-overs" would be expected and none normally takes place. It follows that the above instance is "exceptional" and so "proves the rule." The great majority of fatuoids in which no crossing-over occurs must be due to complex gene mutation.

The above argument is based upon the belief that if a B-chromosome (bearing the fatua factors) mated with a C-chromosome (carrying the sativa factors), then crossing-over between these chromosomes must of necessity take place. But if the B-chromosome is not homologous with the C-chromosome—and certainly

cannot be so in the region bearing the fatuoid complex, there is no apparent reason why crossing-over should take place. Indeed, as Huskins (1932) has pointed out, crossing-over in the "fatua" region should not take place. If the pairing be partial, however, exchange may still take place so as to permit the emergence of the fatuoid complex (see page 68).

Comparing the hypotheses, it will be seen that there is no real conflict between the last two as regards the origin of fatuoids of the B and the C series. There is, however, disagreement as to the origin of fatuoids of the A-series. Until further evidence is obtained, no final decision should be made. In particular, more knowledge of the factors carried not only on the B and C chromosomes, but of the other chromosomes also is required. The recent work of Philp (1933) on the genetics and cytology of sativa and fatua hybrids and of Nishiyama (1935) (see pages 82-83), emphasizes the importance and the difficulty of such work.

RELATION OF "FATUOIDS" TO "WILD" WEED FORMS, AND OF THE "WILD" WEED FORMS TO CULTIVATED OATS.—Malzew in his monograph (1930) points out that a large number of "wild" oats are known, which are mainly found growing in association with cultivated oats, and also with wheat (*e.g.*, *Triticum dicoccum*), Rye and even Barley. These "wild oats" simulate the appearance of the crop in which they are found and as a consequence are very difficult to separate therefrom. Further, like "fatuoid" forms, they tend to ripen simultaneously with the crops, and when harvested with the true grain, do not show delayed germination. The best known of these forms are those belonging to *A. fatua* s.sp. *cultiformis*, and are widely distributed as weeds in cultivated varieties of *sativa*. In the Canary Islands and the Iberian Peninsula, there occurs a single-flowered form of *A. strigosa* (s.sp. *strigosa* var. *uniflora*) which is a special weed of Rye. Its small narrow single grains are very similar to and difficult to separate from the grains of Rye. Similarly, the sub-var. *turgida* of *A. strigosa* s.sp. *strigosa* prol. *brevis* was found by Vavilov to be a special weed of *Triticum turgidum*, in Portugal. It also possesses single grains, but unlike sub-var. *uniflora*, they are remarkably thick and very similar to the wheat grains amongst which they occur.

Malzew further states that comparison of these weed forms (especially the *A. fatua* s.sp. *cultiformis* types) with various specimens of known "fatuoids" reveals no essential differences. He argues that if "fatuoids" are due to mutation (or to chromosome aberration), all so-called "wild" weed oats may have arisen in the same manner, and thereafter been preserved by unconscious but intensive selection.

The argument could be extended. Vavilov found, in the Volga district of Russia, "weed" oats (*A. fatua* (L.) Malz.) in Emmer wheat varying from articulate and readily falling types, through types with dimorphous flowers to types with solidified articulations, *i.e.*, the whole range from non-cultivated to cultivated oats. If the true spontaneous wild oat, therefore, became a weed in the ancient wheat fields, any mutations which took place in the direction of non-shattering, would have been subjected to intensive unconscious selection, resulting in the ultimate multiplication of types which would be harvested and re-sown with the wheat. In other words, essentially "cultivated oats" arose spontaneously and were favoured by selection. (See also page 85.)



**HYBRIDIZATION.**—A considerable number of inter-specific hybrids have been secured. These may be considered under two headings—1: Between species with identical chromosome numbers, and 2: Between species of different chromosome numbers.

1. **BETWEEN SPECIES WITH IDENTICAL CHROMOSOME NUMBERS.**—Many crosses between species with identical chromosome numbers ( $7 \times 7$ ,  $14 \times 14$ ,  $21 \times 21$ ), have been obtained (Surface, 1916; Zinn and Surface, 1917; Love and Craig, 1918; Caporn, 1918; Love and McRostie, 1919; Frazer, 1919; Nishiyama, 1929; Emme, 1929 and 1931; Tschermak, 1929; Ivanof, 1930; Florell, 1931; Kihara and Nishiyama, 1932; Philp, 1933).

In every instance the hybrids appear to have been completely fertile. Irregularity in chromosome behaviour, however, has been noted by Nishiyama (1929), Kihara and Nishiyama (1932) and by Philp (1933). Thus one or two bivalents may lie off the metaphase plate; associations of three chromosomes may occasionally be found and associations of 4 chromosomes more frequently. One or two univalents may often lag and split at the first divisions; at the second division they may lag and pass to the poles at random.

In the hexaploid hybrid *sterilis*  $\times$  *sativa*, Spier (1934) found that multivalent associations were frequent. The chiasma frequency was practically the same as that of its low frequency parent *sterilis*, but statistically significant from that of the *sativa* parent. (Fig. 11.)

Most of the genetical analyses have been concerned, as already noted (pages 31-32), with the behaviour of the linked characters differentiating the species. Philp, in the paper cited above, has extended this type of analysis in the study of certain *fatua*  $\times$  *sativa* crosses. He gives the constitution of the types of the *fatua* species studied as *cs cs BP BP GG P' P' aa* and *cs cs BP BP gg p' p' AA* respectively; and that of the *sativa* species as *CS CS bp bp gg p' p' AA*, carried on five different chromosomes; [where *C* = a factor for basal articulation of the grain with which seven other characters are completely correlated. *B* = a factor for black grain, epistatic to *G* for grey-grain (*bg* together give white grains *B*, *G*, and *C* are independent of one another). *P* = a factor for pubescence on the back of the grain and linked with *B*. *P'* = a second factor for pubescence, independent of *B* and *G* (*bg* together inhibit pubescence). *S* = a factor inhibiting pubescence on the back of the lower grain and is almost completely correlated with *C*. *A* = a factor for short hairs as against *a* = long hairs. In addition, modifying factors are postulated which influence the expression].

2. **BETWEEN SPECIES WITH DIFFERENT CHROMOSOME NUMBERS.**—Here as in wheat the hybrids may be triploid, tetraploid or pentaploid.

A. *Triploid Hybrids.*—Such hybrids have been obtained and studied by Nishiyama (1929 and 1933); Kihara and Nishiyama (1932) and Jones (1932). According to Kihara and Nishiyama (l.c.), seeds develop when the female parent has the lower chromosome number, but none germinate. The reciprocal crosses ( $14 \text{♀} \times 7 \text{♂}$ ) give a low percentage of kernels, but they are plump and may germinate

in some crosses up to 100 per cent. Nishiyama (1929) found the number of bivalents in the cross *A. barbata* ( $n = 14$ ) by *A. strigosa* ( $n = 7$ ) to be 7 to 9. In the later paper (1933), he found  $7'' + 7'$  in the crosses *A. barbata* ( $n = 14$ )  $\times$  *A. strigosa* ( $n = 7$ ) and *A. barbata* ( $n = 14$ )  $\times$  *A. Wiestii* ( $n = 7$ ). The gametes contained 7 to 14 chromosomes, and in the F<sub>2</sub> the diploid chromosome number varied from 14 to 28, constituting an ascending and descending series.

Nishiyama (l.c.) also found trivalents and rare quadrivalents, and Spier (1934) trivalents. In the cross *A. barbata*  $\times$  *A. strigosa* the average number of chiasmata per bivalent was 2.40, whilst those of the parents were 2.10 and 2.16 respectively (Spier l.c.). Both the pairing and the chiasma number, therefore, indicate a very considerable degree of homology between the chromosomes of *strigosa* and seven of the *barbata*. (Fig. 12 (2, a to f).)

Jones (1932 a), in the cross *A. barbata* ( $n = 14$ )  $\times$  *A. brevis* ( $n = 7$ ) obtained segregates exhibiting crossing-over between the equivalent of the "fatuid complex." They showed on the one hand the basal articulation and pubescence of *A. barbata*, associated with the weak awn of *brevis*, and on the other hand the basal articulation and glabrous condition of *brevis* associated with the strong awn of *barbata*. These "cross-over" types were found to have the diploid chromosome number (see page 70).

B. *Tetraploid Hybrids*.—Hybrids of *A. strigosa*  $\times$  *fatua*, *sterilis* and *sativa* with their reciprocals, and also *A. Wiestii*  $\times$  *A. sativa*, have been studied by Nishiyama (1929); Kihara and Nishiyama, (1932). The results were similar to those obtained with triploid hybrids: 7 ( $\text{♀}$ )  $\times$  21 ( $\text{♂}$ ) gave fairly numerous kernels which never germinated: 21 ( $\text{♀}$ )  $\times$  7 ( $\text{♂}$ ) gave very few kernels but 73 per cent. germinated in the case of *A. fatua*  $\times$  *A. strigosa* and 50 per cent. in the case of *A. sativa*  $\times$  *A. strigosa*. All these hybrids grew normally. They were, however, completely sterile when selfed, but a few kernels were obtained from *fatua*  $\times$  *strigosa* when open pollinated. In the pollen mother cells of both hybrids the number of bivalents ranged from 2 to 9 with the mean at 7. In addition many of the cells exhibited 1 to 4 trivalents and sometimes complexes of 4 to 8 elements.

Detailed embryological studies were made on *A. strigosa*  $\text{♀}$   $\times$  *A. fatua* and on *A. fatua*  $\text{♀}$   $\times$  *A. strigosa*. In *A. strigosa*  $\times$  *A. fatua*, the embryo and endosperm started to grow very rapidly. Forty-eight hours after fertilization, however, the endosperm, especially near the embryo, showed abnormality. Free endosperm nuclei united to form chromatin in masses; many vacuoles developed in the cytoplasm; thereafter degeneration proceeded rapidly. On the other hand, the development of the hybrid embryo and endosperm in *A. fatua*  $\times$  *A. strigosa* was markedly retarded. Later, the endosperm tended to increase but soon ceased further development and might dissolve. A regenerative endosperm, however, might develop from the original endosperm near the antipodals. At this stage, the embryo might perish, but some kernels matured. They were somewhat small and tended to be shrivelled.

The following table from Kihara and Nishiyama (1932) summarizes the endosperm development obtained:—

TABLE V.

## THE DEVELOPMENT OF THE ENDOSPERM.

(Data from Kihara and Nishiyama)

Time after pollination.	24 hours.	48 hours.	72 hours.
<i>A. strigosa</i> and <i>A. fatua</i> .	Endosperm develops to some extent.	Endosperm increases more and more.	Cell walls are formed. Endosperm tissue increases remarkably.
<i>A. strigosa</i> ♀ × <i>A. fatua</i> (♂)	Endosperm increases very much, especially in the neighbourhood of the embryo.	Endosperm increases excessively, especially near the embryo. Cytoplasm vacuolates. Some nuclei unite and form large chromatin masses.	Endosperm increases more or less but its degeneration proceeds markedly, <i>i.e.</i> , large or small vacuoles occur numerously and many fused nuclei are dissolving.
<i>A. fatua</i> (♀) × <i>A. strigosa</i> (♂)	Endosperm is weakly formed.	Endosperm increases somewhat but its development is almost stopped. Primitive cell walls are already formed.	Sometimes the original endosperm is already dissolved. The regenerate endosperm is often formed.

C. *Pentaploid Hybrids*.—Such hybrids have been secured by Dorsey (1925), Emme (1929 and 1932), Nishiyama (1929), Ivanov (1930), Kihara and Nishiyama (1932) and Spier (1934). In contradiction to the above results, more kernels tended to be produced when the female parent had the lower chromosome number. The seeds were plump or slightly wrinkled and the germination was good to very good.

The hybrid plants have 35 chromosomes and tend to be sterile. In *A. barbata* × *A. fatua*, according to Dorsey there are 14<sup>II</sup> and 7<sup>I</sup>. On the other hand, Emme (1932) found only 7 to 8 bivalents in *A. Abyssinica* v. *glaberrima* × *A. diffusa* var. *brunnea* and 8 to 9 bivalents in *A. diffusa* var. *iranica* × *A. barbata* var. *typica*. Trivalents may also occur. Nishiyama (1929), in the study of hybrids from *A. barbata* × *A. fatua* and *A. barbata* × *A. sterilis*, obtained results similar to those of Emme. In the cross *A. barbata* (n = 14) × *A. fatua* (n = 21), Nishiyama (1932) found 2 to 11 bivalents. Though markedly sterile, some seeds were obtained by selfing. An F<sub>2</sub> progeny with chromosome complements of 42 to 67 was also obtained by crossing the F<sub>1</sub> with *A. fatua*. The behaviour of the chromosomes in both divisions is similar to that found in tetraploid hybrids (Nishiyama, 1929).

Spier (1934) found that the pairing in the pentaploid hybrid *A. abyssinica* ("naine") × *A. sterilis maxima*, judged by the number of chiasmata, was much looser than in triploid hybrids. More than half the potential bivalents had no chiasmata, 44.5 per cent. had one and 4 per cent. had two. The mean number of bivalents in the parents was 1.87 and 2.26 respectively. (Fig. 12 (1).)

In attempting to explain the relative ease or difficulty in obtaining *Avena* hybrids and the nature and germination of the kernels so obtained, Kihara and Nishiyama (1932) have adopted an explanation which differs from that put forward by Watkins (1932), Thompson (1930), and Thompson and Cameron (1928) in the case of *Triticum* hybrids.

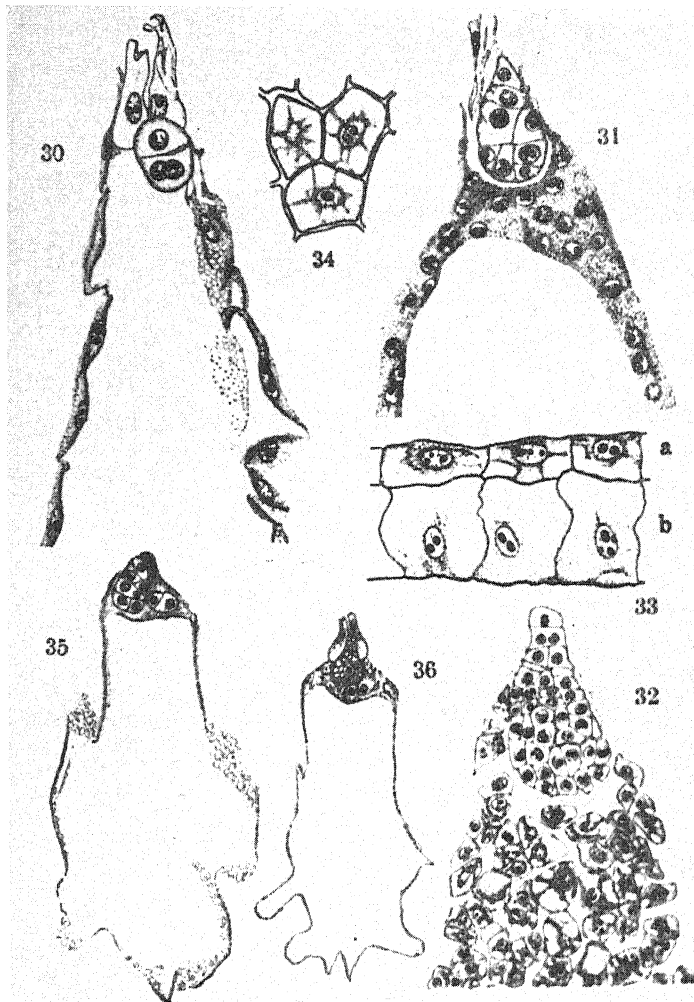


FIG. 20. Development of embryo and endosperm in *A. strigosa* selfed.

30. Longitudinal section of ovule, 24 hours after anthesis. An embryo, two synergids and endosperm present; 31. The same 48 hours after anthesis; 32. The same 72 hours after anthesis; 33. Lateral view of endosperm tissue in the middle of the middle part of the endosperm 72 hours after anthesis. *a.* the first layer; *b.* the second layer. X 440; 34-35 *A. fatua* (♀) × *strigosa* (♂) Longitudinal sections of ovules 24 hours after pollination; 34. Fertilized egg-cell developing, unfertilized polar nuclei adjacent thereto; 35. Unfertilized ovule. X 150. (After Kihara and Nishiyama.)

Following Watkins (1932), this last hypothesis may be summarized as follows : The normal relation of the pollen tube to the style is  $x : 2x$ . If the relation be  $x$  : more than  $2x$ , the growth of the pollen tube is usually normal but may be retarded ; if it be  $x$  : less than  $2x$ , growth is usually greatly reduced. Accordingly, inter-specific pollinations are more likely to succeed when the female parent has the higher chromosome number.

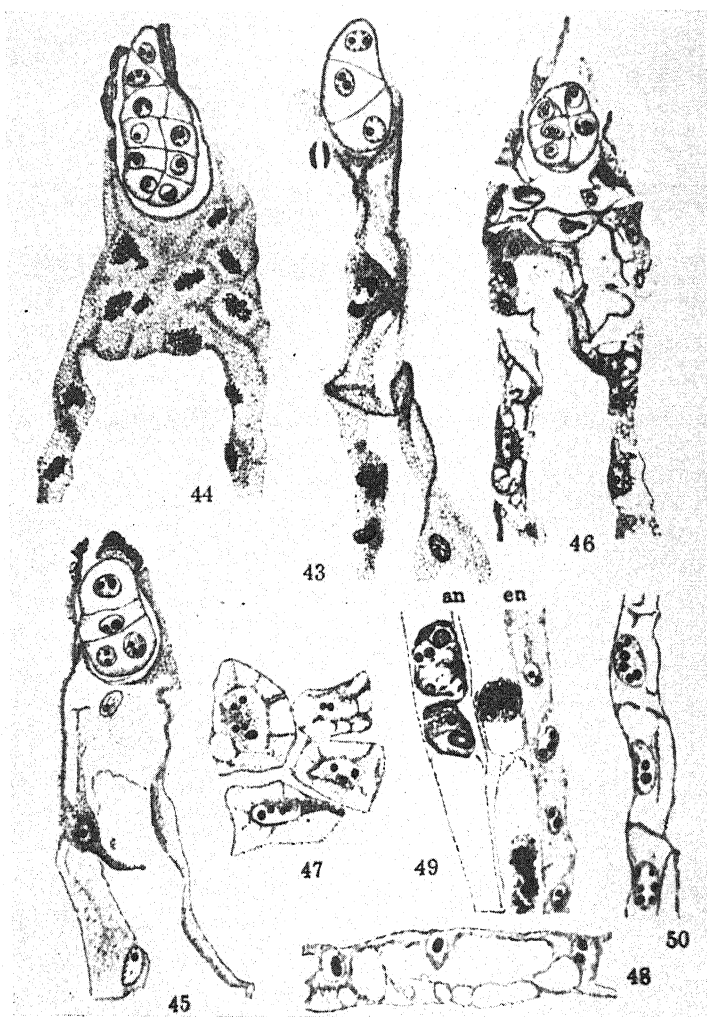


FIG. 21.

43-44. Development of embryo and endosperm of *A. fatua* selfed ; (43) 24 hours after anthesis ; (44) 48 hours after anthesis ; 45-50. The same in *A. fatua* (♀) X *strigosa* (♂) ; (45) 24 hours after pollination ; (46) 48 hours after pollination ; (47) weak formation of cellular tissue near the embryo 48 hours after pollination ; (48) endosperm with many vacuoles in the same ovary ; (49) antipodals (an) and endosperm (en) with dense cytoplasm, 48 hours after pollination ; (50) the endosperm laid on the opposite side to that in 49. Cell wall weakly formed. 43-46, X 340 ; 47-50, X 475. (After Kihara and Nishiyama.)

As to why fertilization does not always follow normal pollen-tube growth, there is as yet no explanation. The quantitative relation between the gametes may be the decisive factor.

As regards endosperm development, the situation depends upon the number of the extra set of chromosomes present. Thus in a cross hexaploid ♀ x tetraploid

♂ the endosperm is  $\begin{cases} ABC \\ ABC (8x) \\ a' b' \end{cases}$ , whilst the embryo is  $\begin{cases} ABC \\ a' b' (5x) \end{cases}$  and these are

nourished by a 6x plant  $\frac{ABC}{ABC}$ . The endosperm is then reduced in size, but

otherwise normal and good germination is found. In the reciprocal cross, the

endosperm is  $\begin{cases} ABC \\ a' b' (7x) \\ a' b' \end{cases}$ , the embryo is  $5x \frac{ABC}{a' b'}$ , both nourished by a 4x plant

$\frac{a' b'}{a' b'}$ . Here, there is only one set of C and the grains are wrinkled with poor germination (see *Triticum*, pages 166-169, for further details).

On the other hand, Kihara and Nishiyama (1932), point out that pollen-tube growth may be normal, weak, difficult or exhibit no growth; and that the stimulus of the male nucleus on the egg and the polar nuclei may be overstrong, normal, weak or produce no effect. (Figs. 20 to 23.) These effects inter-act and produce varied expressions in the nature and germination of the seed. They were unable, however, to formulate any general rule in regard to pollen-tube growth, but in connection with seed development they concluded that in *Avena* (and in *Triticum*) the higher the chromosome number is, the stronger is the stimulus.

The following table summarizes the results obtained.

TABLE VI.  
KERNEL PRODUCTION AND GERMINATION IN AVENA HYBRIDS.  
(Data from Kihara and Nishiyama)

Cross.	Kernel production.	Kernel character.	Germination.
♀ ♂			
2n × 2n.	Easy.	Normal development.	Very good.
4n × 4n.	Moderately easy.	Normal development.	Very good.
6n × 6n.	Easy.	Normal development.	Very good.
2n × 4n.	Moderately easy.	Large size, very shrivelled.	No germination.
Recipr.	A little difficult.	Small size, plump.	Good.
2n × 6n.	Easy.	Large size, very shrivelled.	No germination.
Recipr.	Difficult.	Small size, plump or more or less wrinkled.	Moderately good.
4n × 6n.	A little easy.	About normal development.	Very good.
Recipr.	More or less difficult.	Normal development.	Good.

These results, as they point out, are similar to those obtained by Wakakuwa (1930), with Triticum (see Table XXII, page 168).

The following table shows the relation of the chromosome number in the male nucleus to the chromosome number in the female nucleus (E), and also of the same nucleus to the Polar nuclei (P).

TABLE VII.  
RELATIONSHIP OF CHROMOSOME NUMBERS.  
(Data from Kihara and Nishiyama)

Cross.	$\frac{\text{Male nucleus}}{\text{Female nucleus}} = E.$	$\frac{\text{Male nucleus}}{\text{Polar nuclei}} = P.$
$\begin{matrix} \text{♀} \\ 2n \end{matrix} \times \begin{matrix} \text{♂} \\ 2n \end{matrix}$	$\frac{1}{1} = 1$	$\frac{1}{2} = 0.5$
$4n \times 4n$	$\frac{2}{2} = 1$	$\frac{1}{2} = 0.5$
$6n \times 6n$	$\frac{3}{3} = 1$	$\frac{1}{2} = 0.5$
$2n \times 4n$	$\frac{2}{1} = 2$	$\frac{2}{2} = 1$
$4n \times 2n$	$\frac{1}{2} = 0.5$	$\frac{1}{4} = 0.25$
$2n \times 6n$	$\frac{3}{1} = 3$	$\frac{3}{2} = 1.5$
$6n \times 2n$	$\frac{1}{3} = 0.33$	$\frac{1}{6} = 0.16$
$4n \times 6n$	$\frac{3}{2} = 1.5$	$\frac{3}{4} = 0.75$
$6n \times 4n$	$\frac{2}{3} = 0.67$	$2 = 0.33$

As the table shows, the value of E (male : female nucleus) is  $\frac{1}{1} = 1$  and the value of P (male : polar nuclei) is  $\frac{1}{2} = 0.5$ . The larger the deviation from the normal, the lower is the percentage of germinating kernels. "If the value increases by 2 and 3 times in Avena and Triticum respectively (e.g.,  $2n \text{ ♀} \times 6n \text{ ♂}$  where  $E = 3$ ), viable kernels are never obtained. On the contrary, if the value is reduced to  $1/3$ , small kernels which are able to germinate, are obtained in a low proportion. In other words, the value of E for viable kernels is  $\frac{1}{3} > E < 2$  and  $\frac{1}{3} > E < 3$  in Avena and Triticum respectively. A similar relation also obtains for the value of P (male : polar nuclei)  $\frac{1}{6} > P < 1$  and  $\frac{1}{6} > P < \frac{3}{2}$ " (Kihara and Nishiyama, 1932). (Figs. 20 to 23).\*

ORIGINS OF OATS.—Cytologically, the species of Euavena fall into three groups with 14, 28 or 42 chromosomes. Pairing of the chromosomes within members of the same group is normal, and would thus indicate an allopolyploid origin. Irregularities, however, may occur as Huskins and others have demonstrated.

The first group is constituted by a fairly compact series of species which, nevertheless, differ morphologically. The most ancient types are probably the

\* See also Boyes, J. W., and Thompson, W. P., 1937. The development of the Endosperm and Embryo in Reciprocal Inter-specific crosses in Cereals. J. Genetics, 34 : 203-227.

wild Mediterranean species, *A. clauda* and *A. pilosa*, constituting the series *Inaequaliglumis*. Akin to these are two further wild Mediterranean species, *A. longiglumis* and *A. ventricosa*, with less unequal glumes and markedly elongated calluses. (Series *Stipitatae*.) The remainder of the 14-chromosome group is constituted by certain of the sub-species of *A. strigosa* (*sensu ampl.*).



FIG. 22. Development of embryo and endosperm in *A. strigosa* (♀) × *fatua* (♂).

37. 24 hours after pollination; 38. 48 hours after pollination; 39. 72 hours after pollination; 40. Abnormal formation of cellular tissue of endosperm near the embryo 72 hours after pollination; 41. Vacuolated endosperm in the same ovary; 42. Endosperm with dense cytoplasm in the same ovary. 37-39, X 340; 40-42, X 460. (After Kihara and Nishiyama.)



Here the basic type is s.sp. *hirtula*. It shows affinities with *A. longiglumis*, and according to Malzew is transitional to the remaining sub-species of *strigosa*. Its centre of diversity is again the W. Mediterranean area, and its cultivated derivatives (s.sp. *strigosa* with proles *brevis* and *nuda*) are to be found throughout Western Europe.

The second group with 28 chromosomes is composed of the remainder of the sub-species of *A. strigosa* (*sensu ampl.*). The first s.sp., *A. barbata*, shows affinities with *A. hirtula*. It is unknown in cultivation, but is widely distributed in mountain valleys, on the hill-slopes and in the neighbourhood of cultivated lands from the Canary Islands through the whole of the Mediterranean region to Palestine, Syria, Asia Minor, Tauria, Transcaucasia, Persia, Turcomania, South and East as far as Turkestan, N. Afghanistan and the Western Himalayas. The second s.sp., *A. Wiestii*, is a semi-arid wild form, found in N.W. Africa and Arabia. It too shows affinities with *hirtula*. The third sub-species, *Vaviloviana*, has a more limited distribution and occurs as a weed in Abyssinia and Eritrea. It appears to have given rise to a fourth sub-species, *abyssinica*, (= *A. abyssinica*), which is cultivated in Abyssinia and Eritrea.

The centre of diversity of the second group, therefore, appears to be more or less the same as that of the first, viz., the W. Mediterranean area, but it has spread Eastwards over a much wider area.

Hybrids between members of the first and second group are difficult to obtain. In the cross *A. barbata*  $\times$  *A. strigosa* (s.sp. *strigosa*), the number of bivalents formed was 7 to 9; the hybrids in certain instances were fertile. Jones (1932) in a cross between *A. barbata*  $\times$  *A. brevis* (= *A. strigosa* sp. *strigosa* proles *brevis*) obtained segregates which were diploid and exhibited crossing-over between the linked characters taxonomically differentiating the species.

The evidence, though limited, appears to indicate that there is a fairly close relationship between the members of the first and the second group. If the second or tetraploid group arose by direct doubling, its members would at their inception have been auto-tetraploids. At present, their behaviour is that of allopolyploids. Structural change, however, would in all probability have taken place in the original autopolyploid, and selection would have favoured any change which tended to differentiate the chromosome sets. Competition in pairing would thus be reduced and so lead to greater stability and fertility.

The hexaploid group of oats ( $2n = 42$ ) contains a larger number of species than the diploid and the tetraploids; they are of much greater economic importance; are completely fertile when crossed *inter se* and their chief differential taxonomic characters tend to behave as single factor differences. A fairly close relationship is therefore indicated.

Malzew (1930) has divided the group into two comprehensive species *A. fatua*, L. (s.a.) and *A. sterilis* (s.a.); morphologically they form a parallel series.

The relationship of the hexaploid oats to the diploid and tetraploid forms is obscure. Theoretically, they could have arisen as a sterile cross between a diploid and a tetraploid species. Such triploid hybrids as already noted have been obtained but with difficulty: none as yet has given rise to a fertile hexaploid form.

A few tetraploid hybrids between 14 and 42 chromosomes species have been studied. They are obtained with difficulty (see page 73), and are sterile though they grow normally; 2 to 9 bivalents form at diakinesis, with the mean at 7. There is accordingly homology between certain of the chromosomes in each set.

Pentaploid hybrids have also been studied and are obtained fairly readily, the reciprocal crosses not exhibiting such marked differences as in wheat. The seeds germinate well, but the hybrids tend to be sterile. According to Dorsey,

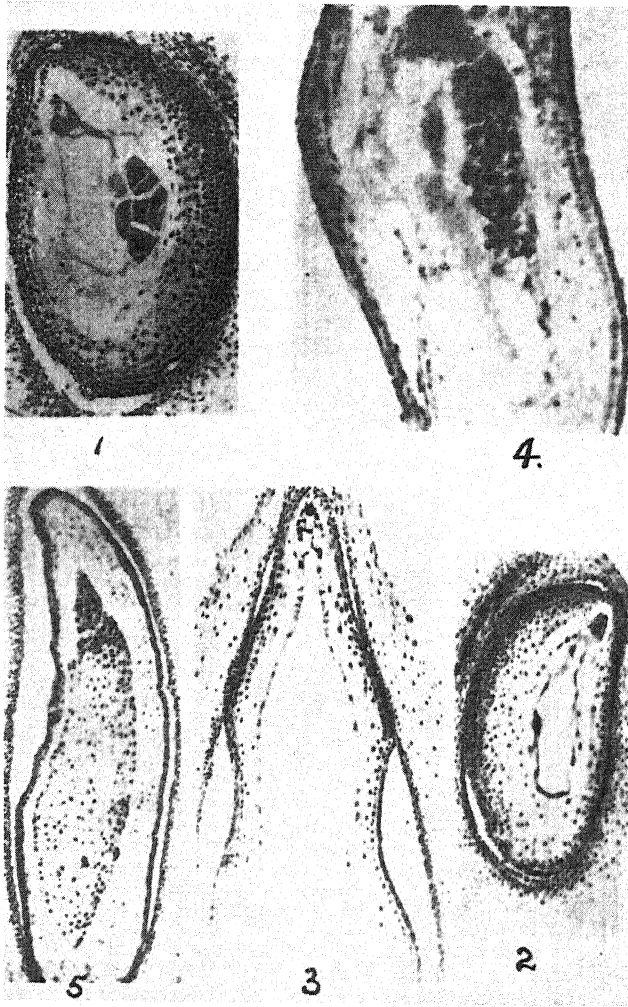


FIG. 23. Development of endosperm in *Avena* hybrids.

1. Unfertilized ovule in *A. fatua* (♀) × *strigosa* (♂) 24 hours after fertilization. X 90;
2. *A. fatua* fertilized by *A. strigosa*, 24 hours after pollination. X 60; 3. The same 48 hours after pollination. X 60; 4. Beginning of the development of the regenerate endosperm. X 120; 5. The regenerate endosperm is formed in the whole embryo-sac. X 40. (After Kihara and Nishiyama.)

there are 14<sup>n</sup> and 7<sup>l</sup>. This would indicate a situation exactly comparable to that found in pentaploid wheat-hybrids. On the other hand, Nishiyama (1932) and Emme (1932) found that the number of bivalents in the hybrids studied by them did not exceed 7 to 8 and 8 to 9 respectively. This would indicate a much lower homology.

Until far more genetical and cytological data is obtained, the relationship between the groups must remain purely speculative. That the members of the hexaploid group are closely related is generally accepted. As we have seen, the general morphology, the parallel variation that is found and the distribution support this conclusion. There is also direct genetical evidence.

*A. sativa* (= s.sp. *sativa*) differs essentially from *A. fatua* (s.sp. *fatua*) by a series of linked factors, as several investigators have shown (Surface, 1916; Love and Craig, 1918; Florell, 1932; Philp, 1933). Similarly, certain of the *nuda* characters in the cross between *A. nuda* (probably = *A. fatua* s.sp. *sativa* proles *chinensis*) behave as if they were due to single factor differences. (Surface, 1917, Caporn, 1918; Love and Mc. Rostie, 1919.) This, however, is only what would be expected, since "nuda" types in reality occur in all the sub-species of *A. fatua* (s. *ampl.*) and can be regarded as the extreme expression of the genotypes in this respect. Also, both Shegalov and Philp (1933) have found plants with nuda characters in the subsequent generations of *sativa* × *fatua* and other crosses. Again, in *A. sterilis* × *A. sativa* crosses, Shegalov (quoted by Philp, 1933) found the *sativa* characters partially dominant to the *sterilis* characters and behaving as single factor differences. On the other hand, the characters of *sterilis* are partially dominant to *fatua*, and in the cultivated *sterilis* derivatives (*A. Byzantina* = *A. fatua* s.sp. *byzantina*), the *sativa* characters are partially dominant to the *byzantina*. (Frazer, 1919; Florell, 1932.)

Several attempts have been made to define the chromosomes concerned.

Thus Philp (1933) has suggested that the chromosome constitution and complexes of the four main hexaploid oats might be represented as follows.

TABLE VIII.  
CHROMOSOME CONSTITUTION OF HEXAPLOID OATS.

(Data from Philp)

<i>A. sativa</i> (= <i>A. fatua</i> ss. <i>sativa</i> ).	<i>A. nuda</i> (= <i>A. fatua</i> ss. <i>sativa</i> ? <i>chinensis</i> ).	<i>A. fatua</i> (= <i>A. fatua</i> ss. <i>fatua</i> ).	<i>A. sterilis</i> (= <i>A. sterilis</i> ss. <i>byzantina</i> ).
ABCZz <sup>n</sup> ABCZz <sup>n</sup> or ABCz <sup>n</sup> ABCz <sup>n</sup>	ABCzz <sup>n</sup> ABCzz <sup>n</sup> or ABC <sup>n</sup> z <sup>n</sup> ABC <sup>n</sup> z <sup>n</sup>	Ac <sup>1</sup> cZz <sup>n</sup> Ac <sup>1</sup> cZz <sup>n</sup> or Ac <sup>1</sup> cz <sup>n</sup> Ac <sup>1</sup> cz <sup>n</sup>	ABc <sup>s</sup> Zz <sup>n</sup> ABc <sup>s</sup> Zz <sup>n</sup> or ABc <sup>s</sup> z <sup>n</sup> ABc <sup>s</sup> z <sup>n</sup>

where A represents a chromosome carrying the sterilis complex.

„ B	„	„	„	„ fatuoid	„
„ c <sup>1</sup>	„	„	„	„ fatua	„
„ C	„	„	„	„ sativa	„
„ c	„	„	„	„ fatua	„
„ c <sup>s</sup>	„	„	„	„ sterilis	„
„ z <sup>n</sup>	„	„	„	„ nuda	„
„ Z	„	„	„	„ complex epistatic to the nuda complex.	
„ C <sup>n</sup>	„	„	„	„ sativa and nuda complexes more than 50 units apart.	

[Philp also makes the further postulates : that the A chromosomes of the four species have some degree of homology with one another and similarly the z<sup>n</sup> chromosomes, the B and c<sup>1</sup> chromosomes, the C, C<sup>n</sup>, c and c<sup>s</sup> chromosomes, and, if present, the Z and z-chromosomes ; also, that the B and C are homologous though probably only to a slight extent, also either the Z or C, C<sup>n</sup>, c, c<sup>s</sup> and z<sup>n</sup> chromosome ; that if C be assumed to carry the complex epistatic to the nuda complex, Z is not required ; that of the four chromosomes, A, B, C, z<sup>n</sup> in sativa, three must have some slight degree with one another—namely B, C, and z<sup>n</sup> ; that the A-chromosome may be a different member of the basic set of 7 and have obtained the sterilis complex by translocation ; if, however, the Z-chromosome carries the complex epistatic to the nuda complex, then A, B, and C may be assumed to be somewhat similar to one another, with B more akin to C than A and Z and z<sup>n</sup> representing a different member of the basic set of 7.]

The above scheme is at the moment highly speculative ; nevertheless, it is along such lines that progress will be made.

TABLE IX.  
STEM SPECIES *A. fatua* L. (*s.ampl.*).  
(After Malzew.)

Nodes pubescent.		Nodes non-pubescent.		
		Spks. large.	Spks. medium.	Spks. plump.
Non - cultivated Sub-species.	s.sp. <i>septentrionalis</i>	s.sp. <i>meridionalis</i>	s.sp. <i>fatua</i>	s.sp. <i>cultiformis</i> .
Distribution.	Mountains of Asia (chiefly the Pamirs) ↓	S.W. Asia to Egypt. ↓	S. Russia and Europe. ↓	N. and C. Europe N. America. ↓
Cultivated Sub-species.	s.sp. <i>nodipilosa</i> proles <i>decorticata</i> .	s.sp. <i>macrantha</i> proles <i>nudata</i> .	s.sp. <i>sativa</i> , proles <i>chinensis</i> .	s.sp. <i>praeagravis</i> , proles <i>grandiuscula</i> .
Distribution.	Mongolia, Siberia, N. Russia ( <i>nuda</i> forms in Mongolia and N. China).	Persia, Transcaucasia, Asia Minor.	S. and C. Russia, W. Europe, N. America (common).	N. and C. Europe N. America.

Philp concludes "that hybridization, polyploidy, structural change and gene mutation have taken place in the evolution of the different hexaploid oat species"; and that structural change and gene mutation involving a small group of chromosomes more or less common to all the species have mainly been responsible. Further, "gene mutations have also altered the phenotype and natural selection assisted by geographical and structural isolation may account for a large number of forms which are only modifications of the principal species."

These conclusions are not necessarily in conflict with the work of the Russian School. Thus on the basis of morphology and distribution, the inter-relationships of the hexaploid oats (following Malzew) could be represented in the manner shown in Tables IX and X.

The fundamental type here appears to be s.sp. *septentrionalis*, and the main centre of diversity of the whole species South-Western Asia.

TABLE X.

STEM SPECIES *A. sterilis* L. (s. ampl.).

(After Malzew)

Nodes pubescent.		Nodes non-pubescent.	
		Spikelets large.	Spikelets small.
Non - cultivated Sub-species.	s.sp. <i>trichophylla</i> .	s.sp. <i>macrocarpa</i> .	s.sp. <i>Ludiviciana</i> .
Distribution.	Asia Minor.	Mediterranean Region, inclusive	Mediterranean region, East to Afghanistan and the mountains of S.W. Asia.
	↓	↓	↓
Cultivated Sub-species.	s.sp. <i>nodi-pubescens</i> .	s.sp. <i>Bysantina</i> proles <i>denudata</i> .	s.sp. <i>pseudo-sativa</i> .
Distribution.	Asia Minor.	Mediterranean region, and introduced elsewhere.	Switzerland (Uruguay).

There is here a transition from East to West with the chief modern centre in Asia Minor. Nevertheless, Malzew is of the opinion that the original centre of diversity was S.W. Asia. If this be accepted, the whole of the hexaploid group arose in the same area.

There is thus a marked difference between the centres of diversity of the species belonging to the diploid and the tetraploid groups and that of the hexaploid group. These centres lie approximately on, but at opposite ends of, the same latitude (the W. Mediterranean area as against S.W. Asia). Nevertheless, if the hexaploid oats arose by polyploidy, primitive ancestors must have been in contact in more remote times. As the evidence indicates that the diploid and tetraploid

oats are more primitive than the hexaploid, the tendency for the members of the first two groups (especially the second) to migrate eastwards, would thus indicate the Western area as the original centre of all.

The precise problem of the relation of the wild species to the cultivated species remains. Here the essential difference lies in the fact that all non-cultivated species are articulate whilst the cultivated are non-articulate. The difference is fundamental. Had the change not taken place, it would have been wellnigh impossible to harvest the oat grain, and the plant would have remained uncultivated.

The archæological evidence indicates that oats were cultivated (or used by man) at a very early date in Europe. The earliest remains probably consist of grains of *A. strigosa* s.sp. *strigosa* found in the lake dwellings of Switzerland. Latter remains appear to belong to *A. fatua* s.sp. *fatua* and to *A. fatua* s.sp. *sativa*.

On the other hand the historical evidence indicates that the cultivation of oats is comparatively recent. There is no evidence that it was known to or cultivated by the Egyptians or the early Eastern peoples. Up to the Christian era, the plant is referred to only as a weed. Thereafter it is noted as cultivated in Central and Western Europe as a grain crop and as a fodder crop in Asia Minor. Its economic importance at the present day in Europe (and in the newer countries) is the result of a gradual increase in its cultivation since the first century A.D.

A few of the earlier writers, Pliny in particular, refer to oats as a weed, which infested other crops (barley especially) to such an extent that it began to be sown and cultivated as such. This early hypothesis may indeed be true. The oat plant in the so-called wild state is always adventive; the nearest relatives to the cultivated forms are to be found in the neighbourhood of cultivation frequently occurring as weeds. These non-cultivated forms, however, are articulate, shedding their grain with ease. If any such type present as a weed in the more ancient crops—barley and wheat—became “non-shedding” under suitable climatic conditions, its ultimate adoption as a grain crop would be wellnigh inevitable. Man accordingly used what was already to hand. The situation would be comparable to that of rye, regarded by Vavilov as also a “weed” segregation out of wheat.

Now the essential difference between non-cultivated and cultivated oats lies in the fact that the former are shedding types and the latter “non-shedding.” In a shedding type either the spikelet as a whole is articulate, the lemma of the basal floret possessing a callus and a cicatrix or scar, or alternatively all the florets are articulate, the lemma of each floret developing a callus and a cicatrix or scar. In the non-shedding, cultivated types, the articulation is solidified, the callus and the cicatrix markedly reduced or absent. This difference when studied genetically is found to be associated with other characters, generally referred to as the “wild complex” (see page 62).

The “wild complex” (presence of articulation, etc.) appears to be dominant to the “cultivated complex” (absence of articulation, etc.) in all diploid and tetraploid hybrids (Emme, 1934), but not in hexaploids. This would indicate that the cultivated types first arose as recessive mutations in species with the lower chromosome number. In hexaploids, however, the cultivated type is partially dominant to *fatua*; (see pages 31 and 63), and would thus suggest that the cultivated type arose as a dominant mutation. Polyploidy, however, may be obscuring the position.

Huskins' "chromosome aberration hypothesis" of the origin of fatuoids indicates that structural change in the chromosomes may have played a very important part, and reference to Philp's hypothetical formulæ for the chromosome complexes of the hexaploid oats (see page 82) indicates how complex and how little understood the situation is. The hexaploid oats are polyploids and though auto-syndesis appears to be the rule, allosyndesis is also possible. In "structural change" of the chromosomes combined with gene mutation, must be sought the final solution.

Whether oats came into cultivation in the above manner or more indirectly, the fact remains that three centres of origin must be postulated. This explains why the earlier authorities advanced arguments in favour of three separate centres, viz., W. Europe, E. Europe, and Central or S.W. Asia. In a measure all were correct. The error lay in ascribing the origin of all the cultivated oats to one centre.

Bringing together the data, the situation may be visualized in the following manner.

### I. *A. strigosa*, Schreb. s. ampl.

Wild.	Cultivated.
1. s.sp. <i>hirtula</i> ( $x = 7$ )	s.sp. <i>strigosa</i> , <i>nuda</i> types incl. <i>brevis</i>
2. s.sp. <i>Vaviloviana</i> ( $x = 14$ )	s.sp. <i>abyssinica</i>

### II. *A. fatua*, L. s. ampl. ( $x = 21$ )

Wild.	Husked.	Nuda.
1. s.sp. <i>septentrionalis</i>	s.sp. <i>nodipilosa</i>	s.sp. <i>decorticata</i>
2. s.sp. <i>meridionalis</i>	s.sp. <i>macrantha</i>	s.sp. <i>nudata</i>
3. s.sp. <i>fatua</i>	s.sp. <i>sativa</i>	s.sp. <i>chinensis</i>
4. s.sp. <i>cultiformis</i>	s.sp. <i>praegravis</i>	s.sp. <i>grandiuscula</i>

The first s.sp. *nodipilosa* extends from Mongolia and Siberia to the Urals and N. Russia. Its "nuda" form has long been cultivated in Mongolia and N. China. The second s.sp. *macrantha* is as much a weed as a cultivated oat. It is found especially in Persia and Asia Minor. The *sativa* s.sp. is now the most commonly cultivated of all oats. It was the first of the hexaploid oats introduced into Europe, and it is unquestionably of Eastern origin. The fourth s.sp. *praegravis* is cultivated in N. and Central Europe, Central Russia and in Canada and the United States. It too is ultimately of Eastern origin.

### III. *A. sterilis*, L. s. ampl.

Related Wild Form.		Cultivated.	
		Husked.	Nuda.
1.	s.sp. <i>Ludoviciana</i>	s.sp. <i>pseudo-sativa</i>	
2.	s.sp. <i>trichophylla</i>	s.sp. <i>nodipubescens</i>	
3.	s.sp. <i>macrocarpa</i>	s.sp. <i>byzantina</i>	s.sp. <i>denudata</i>

*Pseudo-sativa* is at present known only in Switzerland. Of the others, s.sp. *nodipubescens* is distributed in Asia Minor, and *byzantina* in the Mediterranean region.

## CONCLUSIONS.

1. The original centre of diversity of the Euavenas was probably the Western Mediterranean region.

2. The species are polyploid, with representatives having 7, 14 and 21 haploid chromosomes.

3. The most primitive group consists of wild species with 14 chromosomes having its centre of diversity in the W. Mediterranean area. It has no cultivated representatives.

4. The closely allied form *A. strigosa* s.sp. *hirtula*, also found in the W. Mediterranean region, probably gave rise to the primitive cultivated forms s.sp. *strigosa* with proles *brevis* and *nuda* ( $x = 7$ ).

5. Geographical migration to the East, gave rise to (? autopolyploid) species with 14/28 chromosomes. Of these, *Vaviloviana* may have given rise to the cultivated s.sp. *Vaviloviana*.

6. The hexaploid oats arose in the East (S.W. Asia), and are probably allopolyploids. They overlapped, however, with the tetraploid forms in a Westerly direction.

7. The cultivated oats are of fairly recent origin and may have arisen in three centres as "non-shedding" mutant forms in older cultivated grain crops such as barley and emmer.

8. The relationship between "non-shedding" and "shedding" oats is still obscure.

9. This relationship may, perhaps, be solved by a critical study of the "complex" differentiating s.sp. *hirtula* from s.sp. *strigosa*. In these forms, the situation is not complicated by the polyploid condition.

ECONOMIC USES OF OATS.—Oats are sometimes grown for pasture and as a green crop for hay. The grain is a valuable horse feed, and as rolled oats, or oatmeal is very extensively used as a human diet. The following tables indicate the composition :—

TABLE XI.

THE COMPOSITION OF THE CARYOPSIS OF OATS COMPARED WITH THAT OF WHEAT.

	Crude Protein.	Crude Fat.	Nitrogen free Extract.	Crude Fibre.	Ash.
	Per Cent.	Per Cent.	Per Cent.	Per Cent.	Per Cent.
Wheat ..	13.9	2.5	78.2	3.4	3.9
Oats ..	14.2	6.8	75.4	1.4	2.3

TABLE XII.

THE COMPOSITION OF THE OAT HUSK.

Protein.	Oil.	Carbohydrates.	Fibre.	Ash.
Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
2.1	0.81	55.7	35.8	5.2



TABLE XIII.

THE COMPOSITION OF THE THREE CEREAL GRAINS AS THRESHED.

(Data from Kellner)

	Moisture.	Crude Protein.	Crude Fat.	Nitrogen free Extract.	Crude Fibre.	Ash.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Wheat ..	13.4	12.1	1.9	69.0	1.9	1.7
Barley ..	14.3	9.4	2.1	67.8	3.9	2.5
Oats ..	13.3	10.3	4.8	58.2	10.3	3.1

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## CHAPTER IV

### THE WHEAT SPECIES (TRITICUM)

THE wheat plant is an annual cereal. Two seasonal forms are recognized, winter wheat and spring wheat. Under the warmer climatic conditions, all wheats are winter grown.

ROOTS.—The root system as a whole is fibrous and may be divided into two types—the seminal or primary roots and the adventitious or secondary roots.

1. SEMINAL ROOTS.—The seminal roots belong initially to the embryo or develop later from the base of the “mesocotyl.” The primary root is the developed radicle. From the sides of the axis about the level of the epiblast, a pair of lateral rootlets develop; a second pair emerge later in the same plane and just above the first pair. According to Percival (1921), a sixth rootlet may develop

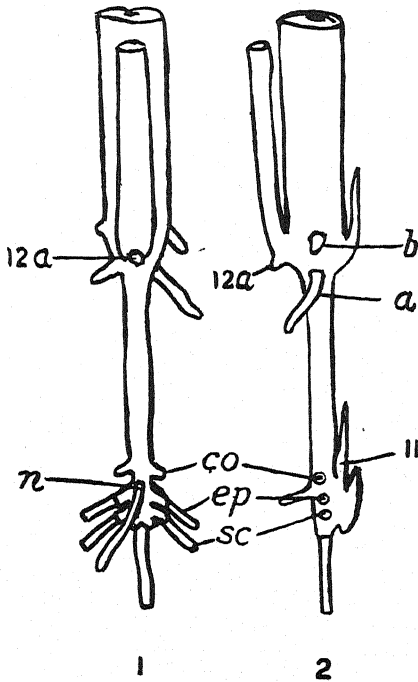


FIG. 24.

Arrangement of the seminal roots and the adventitious roots at the “tillering” node of a young plant. *sc*, Scutellum pair; *ep*, epiblast pair; *co*, coleoptile pair; *a*, one of the pair of roots at first node of primary stem; (*b*), one of the pair at second node of primary stem; *11*, first branch of primary axis; *12a*, one of pair of roots at first node of second branch of primary axis. (After Percival, *The Wheat Plant*, by special permission of the author.)

at right angles to the first pair from a point on the axis above the epiblast. If it develops at all, it appears after the others have attained a considerable length, and it may or may not be preformed in the embryo. Finally, one, two or even three roots, not preformed in the embryo, may be produced above the insertion of the coleoptile. This gives a maximum total of five to six true seminal roots. (Fig. 24.)

Wiggans (1916) reports that the number of secondary roots is by no means constant. Walworth and Smith (1918) examined eleven varieties of wheat and found that, omitting the primary radicle, nine of them had the nodal number at two and two at four.

The apex of each of these roots is smooth and pointed, the extreme tip protected by a root-cap. For a short distance just beyond the tip the surface bears many thousands of delicate root-hairs.

The seminal roots are at first thin and of nearly uniform diameter. Later, the surfaces shrivel and the diameter is greatly reduced. When from 4 to 6 inches long, many fine lateral rootlets develop.

Earlier writers regarded these roots as functional for only a short period of

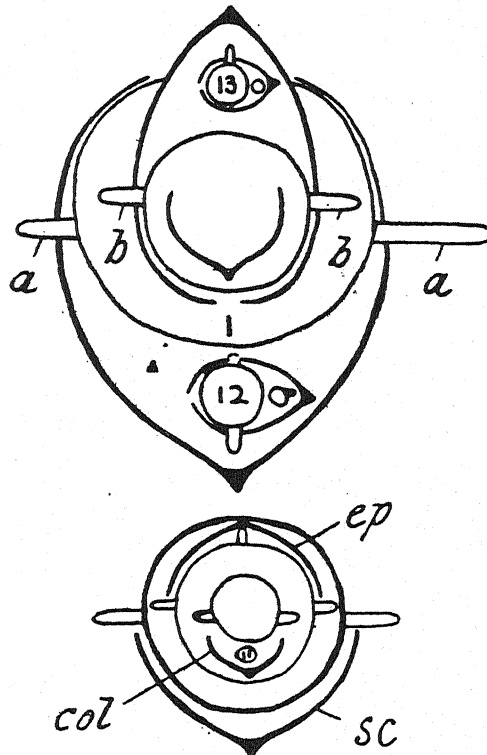


FIG. 25. Diagram of the arrangement of the roots, leaves and stem axes in Fig. 24.

Below : the position of the first three pairs of seminal roots and the seventh root ( $n$  in Fig. 24) in relation to scutellum ( $sc$ ), epiblast ( $ep$ ) and coleoptile ( $co$ ).

Above : relation of first adventitious roots to primary axis (1), and to first (12) and second (13) tillers. (After Percival, *The Wheat Plant*, by special permission of the author.)

time, "being concerned with the absorption of water for the growth of the young plant, especially in its earliest stages." Robbins (1924) states: "It (the whorl) usually dies before the plant is full grown." On the other hand, Rostmistrov (1909) says, "these primordial rootlets continue to be the main roots of the first order during the whole period of vegetation which follows." Weaver (1926) confirms this statement. The seminal roots "continued to grow and function

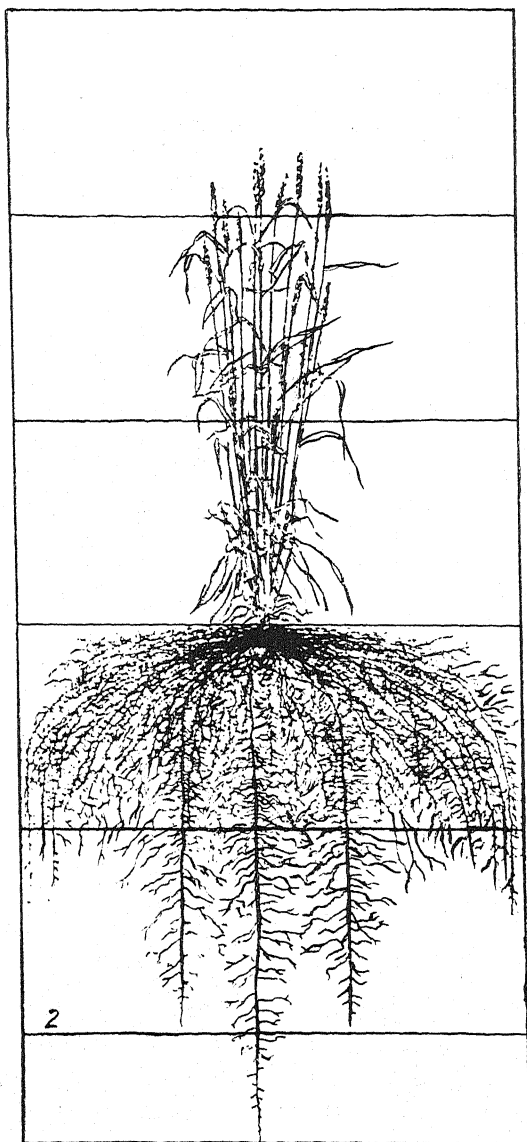


FIG. 26.

A Marquis wheat plant growing without competition at Saskatoon in 1931. It bore 14 stems, all headed, 98 crown roots and 5 seminal roots. It was still green when the ordinary crop was ripe. (After Simmonds and Sallans.)

until the plant matured, at which time they had reached greater depths than any of the roots that formed later." Also, amputation of the seminal roots seriously interferes with subsequent growth and yield (Simmonds and Sallans, 1930; Todaro, 1931). Weaver also reports that a few of these roots grow vertically downwards, reaching a maximum depth in one instance of 7.4 feet. They develop short laterals almost throughout their length. The remainder of the seminal roots grow out obliquely to a distance of 0.5 to 1.3 feet and then zig-zag vertically downwards for a distance of several feet. They, too, branch almost throughout.

Worzella (1932) found that the seminal roots of non-hardy winter wheats tended at first to grow out more or less horizontally, and at a later stage turned downwards. In most of the hardy types examined, the tendency was for most of the seminal roots to grow obliquely outwards or straight downwards. The adventitious roots did not develop to any extent until spring.

Locke and Clark (1924) reported the finding of wheat plants growing, it should be noted, under abnormal conditions, which possessed no secondary roots but developed to maturity on the seminal roots only.

According to Krassovsky (1926) the primary root system chiefly serves the central axis of the plant, whilst the adventitious roots mainly function in relation to the tillers. A similar situation was indicated for barley and rye.

We must, therefore, conclude that the seminal roots of the wheat (and probably of all annual cereals) are functional throughout the life of the plant.

2. ADVENTITIOUS ROOTS.—Avery (1930) states that roots occasionally appear at variable points in the interval between the level of divergence of the scutellum and that of the coleoptile. These roots may be the third pair of roots which later develop above the first and second pair of seminal roots, and "a corresponding opposite rootlet frequently developing from the base of the axillary bud of the coleoptile" (Percival, 1931). McCall (1934) also states that one, two or three roots may form above the insertion of the coleoptile. If these roots be not preformed in the embryo and arise above the insertion of the scutellum, they would appear to constitute the first adventitious roots. The normal adventitious roots develop from the nodes of the main axis and its branches near the ground level. The first of these roots to form is a pair which grows out from the first tillering node of the main axis, one to the right and one to the left of the first lateral bud. At the second tillering node a similar pair arise, succeeded higher up, where the internodes begin to lengthen, by a whorl of 4 to 6 roots, more or less symmetrically arranged. The plane of the roots from the lower nodes is parallel to the plane of the paired seminal roots. (Fig. 24 and 25.)

The lateral axes or tillers develop a similar series of adventitious roots, but instead of a pair of roots developing at the basal node, only one forms. Further, the roots on any one axis are arranged at right angles to the plane of the roots of the previous axis. Thus the plane of the roots of the first lateral cuts the plane of the roots of the primary axis at right angles—i.e., it is in the same plane as the sixth seminal root. (Percival, 1921.)

In this way a very large number of secondary roots are produced. The adventitious roots are somewhat thicker than the seminal. They are at first unbranched and covered almost throughout their length with root-hairs, thus corresponding to the so-called "white" roots in barley. Later, numerous lateral



rootlets appear, and with their development the root-hairs disappear, except towards the apex, and the roots themselves become thinner and brown in colour.

The first tendency of the adventitious roots is to spread laterally, the angle depending in part on the variety and, to a marked degree, on the soil conditions.

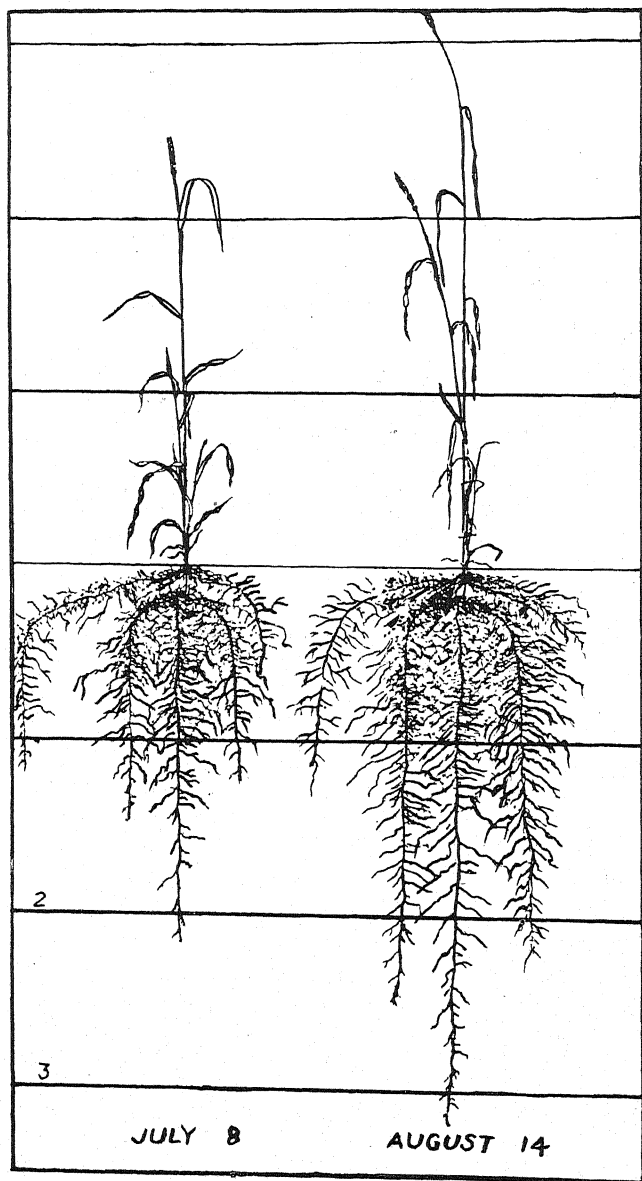


FIG. 27. Root systems of Wheat.

The development of Marquis wheat at Indian Head at mid-season and at harvest time in 1932, the plants growing under ordinary field conditions. The development of the crop was favourable although suffering somewhat from drought because of insufficient reserve soil moisture. (After Simmonds and Sallans.)

Thereafter, the roots grow downwards, filling the upper 2 to 3 feet of the soil with a dense mass of rootlets. (Figs. 26 and 27.)

Winter wheats are in general deeper rooted than spring wheats. The mature root system has a working depth of 3.5 to 4 feet and a maximum depth of 5 to 7 feet. (Weaver, 1926.) About 60 per cent. of the whole root system occurs in the first 12 inches of soil.

The extent of the root system is markedly influenced by the texture of the soil, the relative fertility and the water supply. Some evidence of varietal differences has been noted but there is as yet no definite information.

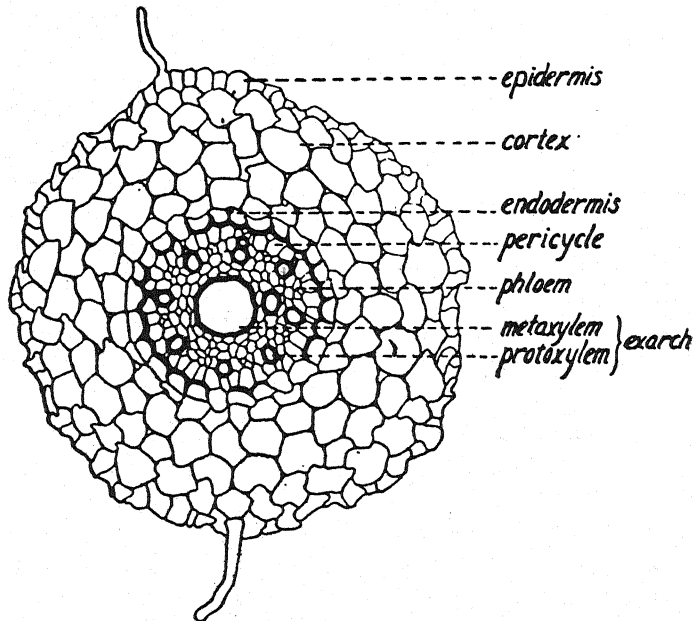


FIG. 28. Transverse section of Primary Seminal Root. (After Avery.)

Recently, an attempt has been made to evaluate the competitive effect of weeds on the root system of certain of the cereals. (Palychenko and Harrington, 1934.) Many noxious weeds, *e.g.*, wild mustard, have more extensive root systems and greater assimilative surfaces (at 21 days) than any of the cereals. Wild oats is a serious competitor but its effect is reduced by the fact that it has slow germination, few primary roots, and can only establish itself very slowly.

**ANATOMY OF THE ROOT.—1. SEMINAL ROOT.**—The young seminal root shows three distinct tissues.

a. *Piliferous layer.*—A continuous outer layer consisting of thin elongated cells, many of them developing into root-hairs.

b. *Cortex.*—Six to eight layers of parenchymatous cells with small intercellular spaces. The innermost layer of the cortex is differentiated as the endodermis, a single layer of unbroken closely-fitting cells. The outer wall of these cells is thin; the inner is somewhat thickened and the radial walls also slightly thickened.

c. *Vascular Cylinder*.—The vascular cylinder is polyarch. Externally a single layer of cells constitutes the pericycle. Its cells are at first comparatively thin-walled, and are of nearly equal dimensions (the radial diameter being the greater), except at the points opposite the proto-xylem, where the cells are much smaller.

The xylem strands are 7 to 8 in number. The proto-xylem consists of 1 to 2 narrow vessels, 5 to 10 $\mu$  in diameter, with either annular or spiral thickenings. The secondary wood is centripetal, the vessels being larger (15 to 20 $\mu$ ) and the walls pitted.

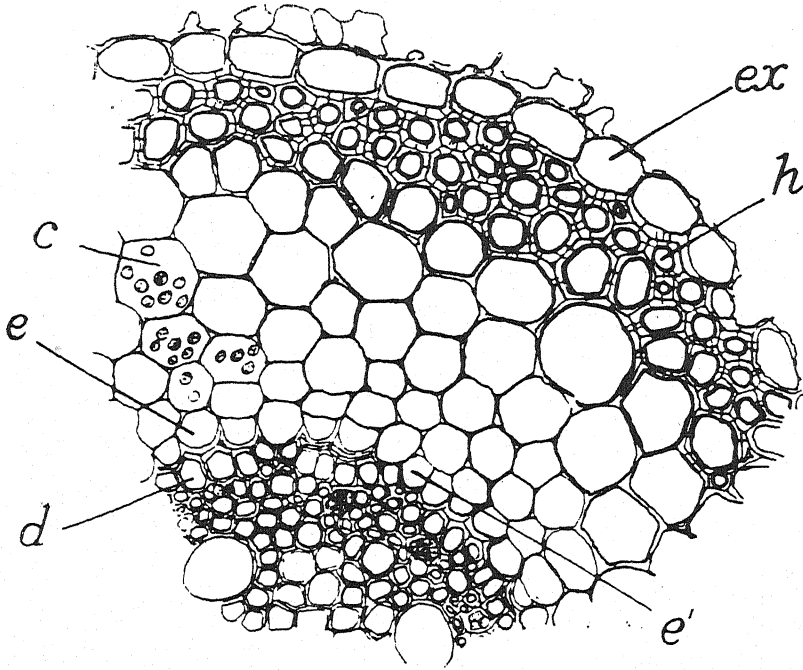


FIG. 29.

Transverse section of a portion of an adventitious root from the node immediately above the soil surface (X 150). *ex*, Exodermis; *h*, thick-walled cortical cells; *c*, thin-walled cortical cells containing chloroplasts; *e*, endodermal cell with thick inner wall; *e'*, thin-walled endodermal cell; *d*, lignified pericycle. (After Percival, *The Wheat Plant*, by special permission of the author.)

The phloem is scanty and consists of a few cells arranged alternately with the xylem strands.

The remainder of the cylinder is filled with moderately thick-walled parenchyma.

In the centre, a large space or duct occurs. This is usually interpreted as being a pitted vessel. In some cases, there is no central duct, but two or more large ducts are irregularly distributed in the tissue. (Fig. 28.)

In an older seminal root, several changes occur.

a. The piliferous layer disappears.

b. The cortical layer immediately below becomes suberized, and for a time acts as a protective exodermis. Later, the greater part of the cortex shrivels and dies.

c. The cells of the endodermis become markedly thickened and cuticularized, the inner walls exhibiting distinct stratification.

d. The walls of the pericycle thicken and lignify.

e. The ground tissue of the stele becomes sclerotic.

2. ADVENTITIOUS ROOTS.—The structure of the young adventitious root is similar to that of the seminal root, but, instead of one central duct, several ducts usually occur, irregularly distributed in the parenchyma of the stele.

As the root ages, an endodermis forms, which is, however, more persistent than that of the seminal root. Below it, two or three layers of the cortex develop a zone of sclerotized tissue, which affords protection to the inner tissues. Perhaps because of this layer, the thickening of the endodermis is much delayed. (Fig. 29.)

The lateral rootlets develop in the pericycle opposite the phloem, not opposite the xylem. (Percival, 1921.)

STEMS.—On germination the hypocotyl remains short. About two weeks later, the interval (inter-node) between the scutellum and the coleoptile elongates slightly. Thereafter, the axis above the insertion of the coleoptile begins to develop, raising the nodes beyond it to approximately ground level (Avery, 1930). It is this region, externally enclosed by the elongating coleoptile, which constitutes the thin erect rhizome. When grains are sown deeply, other inter-nodes above this may lengthen to form part of the rhizome.

The axis once at ground level remains comparatively short for some time, later elongating to a height of 3 to 4 feet or more. The expansion is due to the elongation of the inter-nodes, there being an intercalary growing region at the base of each. The lowest inter-node elongates first, followed by the others in succession.

The ultimate stems are erect, cylindrical, in some types furrowed and either glabrous or scabrous. The nodes are 5 to 7 in number, the average being 6. Each node is contracted and solid. The inter-nodes are generally hollow, but in certain Durums and Rivets among the common cultivated species they are solid. The length of the inter-nodes increases from the lowest upwards to the last, which is always the longest. (See Table XIV.)

The actual length of the stem depends on the variety and the environment. The distance of planting, the amount of water and the nature of the solutes are all factors of importance.

The whole of the lower inter-nodes and much of the upper are covered by the leaf-sheaths.

TILLERING.—The lateral branches of the wheat, as in all grasses, are termed "tillers." They develop from the buds in the axils of the lower leaves attached to the basal crowded nodes.

Even in the embryo the first bud is visible—the coleoptile bud. "This bud in certain varieties and under certain environmental conditions may form a lateral. In normally planted grain, it is usually the second and third buds which develop into laterals, followed by the fourth and fifth buds. Others may develop later. (Fig. 25.)

In deeper planted grain (3 inches and over), the second and third buds generally remain dormant, the first lateral arising from the fourth bud.

The functional buds originate just below or at ground level. They grow slowly at first to form a compact plant of some five shoots. In the axils of the two lowest leaves of the first and second laterals, buds also form, and these buds in turn elongate to form laterals. As a consequence, nine short shoots may be produced, one primary, eight secondary. This process may continue until a very large number may result.

TABLE XIV.  
AVERAGE LENGTH OF INTER-NODES.  
(Data from Percival.)

Inter-nodes.	1	2	3	4	5	6	Total length.
			Red Squarehead.				
Long straws.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Found ..	3.6	8.9	12.3	19.2	30.3	49.8	124.1
Calculated ..	—	7.9	14.0	21.3	34.5	—	—
Short straws.							
Found	2.0	4.6	8.6	14.4	24.0	36.0	89.6
Calculated ..	—	5.3	9.5	16.3	25.2	—	—
			Blue Cone.				
Long straws.							
Found ..	3.4	6.4	10.4	15.6	29.4	60.0	125.2
Calculated ..	—	6.9	11.0	19.9	37.8	—	—
Short straws.							
Found ..	2.1	3.6	6.4	9.9	19.2	39.0	80.2
Calculated ..	—	4.2	6.7	12.8	24.4	—	—

The structure of the laterals reproduces the structure of the primary axis.

FACTORS INFLUENCING TILLERING.—The number of tillers produced is very variable, depending on both internal and external conditions.

1. Inherent characteristics of the variety. Certain types consistently develop more tillers than others.

2. Seeding. Thin seeding promotes tillering; thick seeding reduces it.

3. Size of seed. The plants from large grains tend to tiller more than those from small grains.

4. Available food. Tillering tends to increase with increase of food supply.

5. Environmental factors. Excessive rainfall tends to reduce tillering. Air and soil temperatures may produce marked effects. At low temperatures, tillering is checked.

LODGING.—In severe storms of wind and rain, wheat (and other small-grained cereals) are apt to be "laid." If the plants are still green, they may

re-erect themselves by unequal growth due to gravitational stimulus. Older plants, however, have little power of recovery.

The cause of the lodging is to be found in (a) weakness of straw and (b) weakness of root-hold. The factors inducing this weakness may be inherent in the variety or produced by external conditions.

Two inherent factors are of primary importance.

1. *The nature of the straw*.—Some varieties have short stiff straw ; in others, the straws are longer and more slender, the ears tending to droop.

2. *Nature of the roots*.—a. Many winter wheats possess strong stems which are “kneaded” at the base and carry many adventitious roots. These roots for the first 1 to 2 inches are somewhat stout and rigid, with their cell walls lignified. Such varieties tend to be firmly anchored to the soil.

b. Other varieties, including many of the “spring” wheats, have their tillers erect and crowded, the adventitious roots being thinner, more vertical in growth and less lignified. Such varieties possess less anchoring power.

In a further analysis of the situation, Rivera (1916) concluded that lodging was due in the ultimate to high water content of the tissues. Welton (1928) stressed the reverse condition, *i.e.*, that “lodging results from low dry matter content per unit length of culm.” Now a low dry matter per unit length may result from a relatively low composition of lignin and various reserve materials, such as disaccharides and polysaccharides, or from the development of relatively small slender culms. This condition in turn is due to a low carbohydrate nitrogen relation, the result of shading, hyper-nutrition or relatively high temperatures. Nevertheless Davidson and Phillips (1930) found that though nitrogenous manures decrease the silica and ash content the lignin is increased. In Tubb's experiments, nitrogen deficiency tended to strengthen the lower inter-nodes, whilst a potassium deficiency decreased the strength of the lower nodes but increased the strength of the intermediate nodes. He concluded that weakness of the inter-nodes is due to a loss of strength in the mechanical tissue, and that this mechanical tissue can only develop efficiently in the presence of a sufficiency of potassium.

The chief external factors responsible are :—

1. *Shading*.—If plants are crowded, light is shut off from the stems. The bases of the plants show an etiolation effect, the cell-walls of the tissues being smaller and thinner, and the mechanical tissue much reduced. (Fig. 30.)

2. *Hyper and unbalanced nutrition*.—Heavy dressings of nitrogen and excess of water produce a similar relation. Lack of potassium induces weakness in the mechanical tissue.

3. *Temperature*.—Relatively high temperatures tend in a similar direction.

4. *Disease*.—Several fungus diseases may directly induce stem weakness.

The effect of the environment varies with the developmental stage of the plant (Kraus, 1910). In oats, Stanton et al. (1928) found on the whole that there is less lodging with mid-season varieties, whilst Florell (1929) in California found that lodging decreased in wheat, oats and barley when spring sown.

Much work has been done in the breeding of types which are resistant to

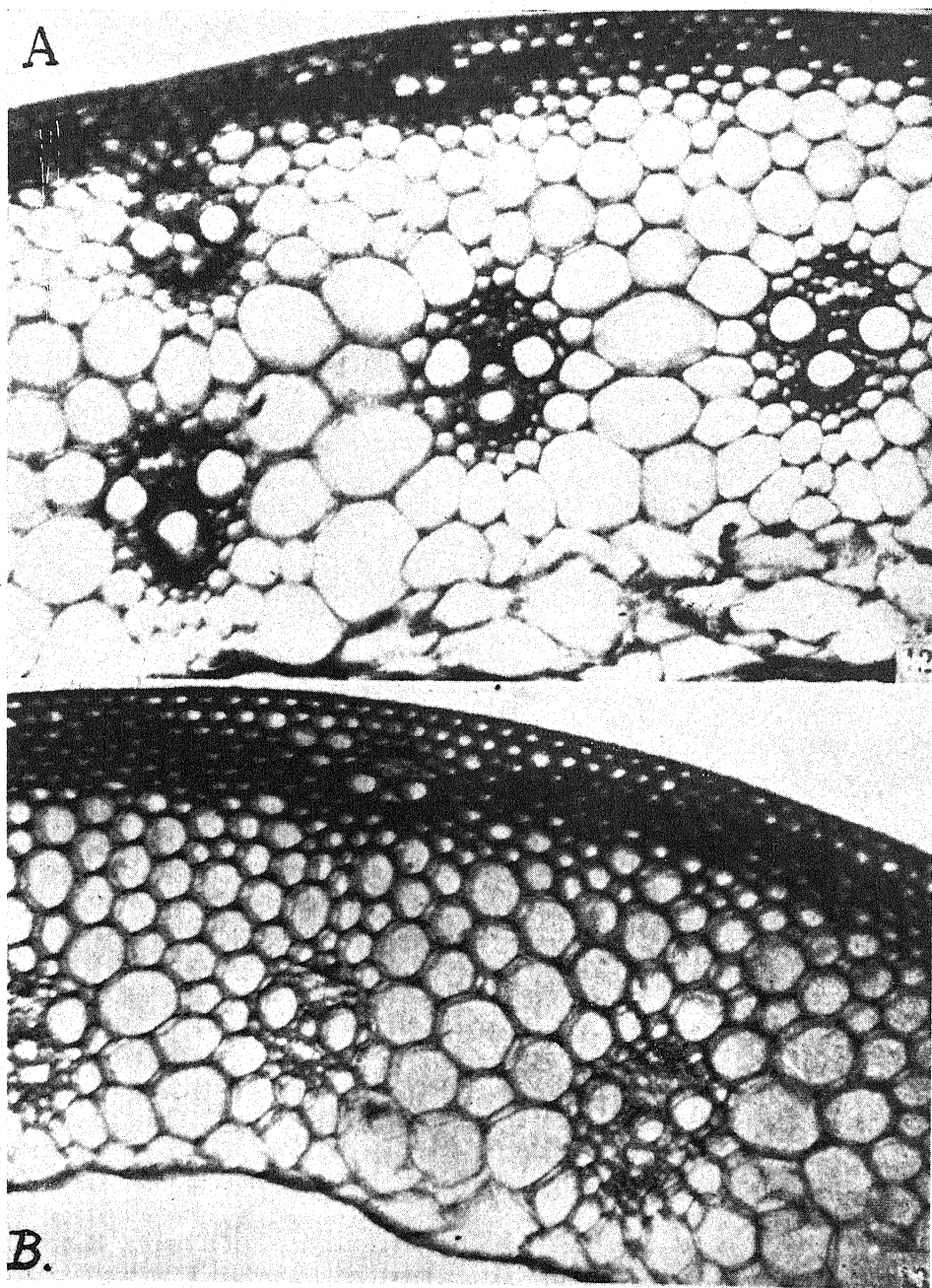


FIG. 30.

Transverse sections of wheat culms showing differences in relative development of tissues : A, thin seeding, diameter greater than in B, cells more completely lignified. B, thick seeding, total diameter less, lignification less complete. (After Welton.)

lodging, and some analysis of the genetical situation has been attempted. (For detailed Bibliography, see *Lodging in Cereals*, Imp. Bur. Plant Genetics.)

ANATOMY OF THE STEM.—Five distinct tissues may be recognized without difficulty.

1. EPIDERMIS.—The epidermis is formed of narrow elongated cells with short square cells intercalated at intervals. The walls are much thickened and pitted. Exposed surfaces are covered with a cuticle and the cuticle, in glaucous

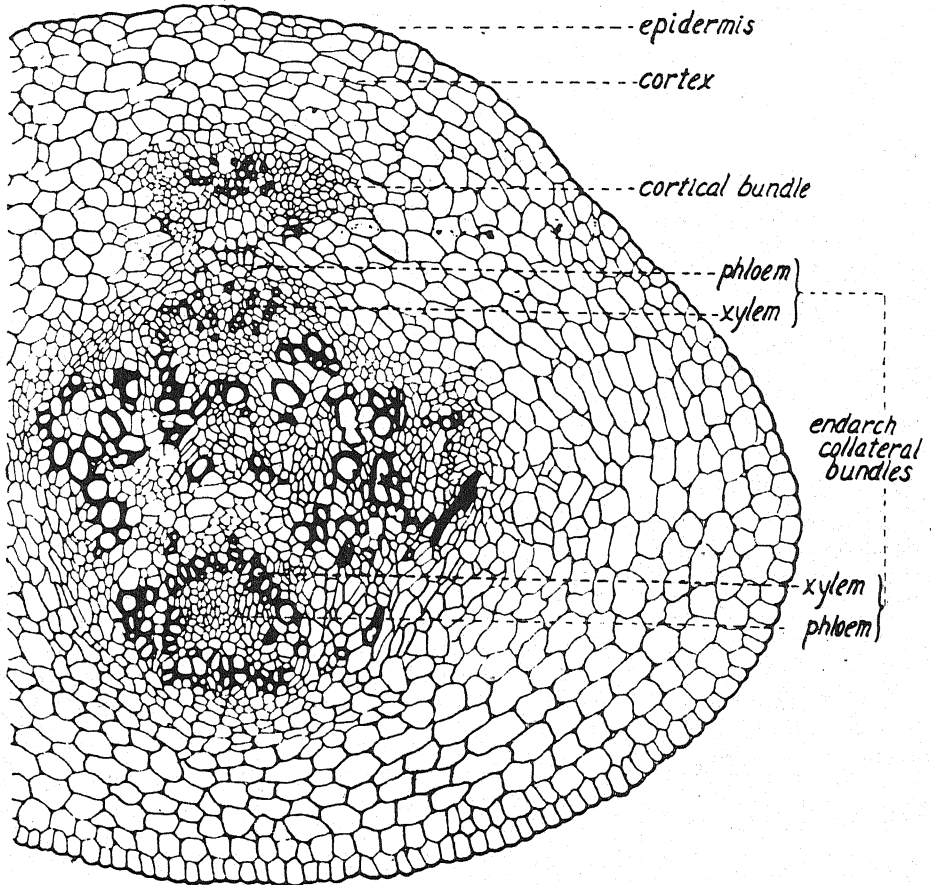


FIG. 31. Transverse section of lower part of "first inter-node" of four-weeks-old plant, showing transition. (After Avery.)

types, is coated with minute flakes of wax. Single or double lines of stomata, similar to those of the leaf, may occur.

2. HYPODERM.—A cylinder of mechanical tissue lies immediately beneath the epidermis. It is of variable thickness, the inner margin being more or less wavy. It is composed of lignified fibres with thick walls (about  $4\mu$ ) and narrow lumina.

3. CHLOROPHYLL OR ASSIMILATING TISSUE.—This tissue occurs as parallel bands embedded in the hypoderm. The bands may coalesce and they gradually



thin out as they pass downwards below the leaf-sheaths. Each band abuts on the epidermis on its inner face, and is in communication with the exterior via the stomata. It is composed of delicate parenchymatous cells, irregular in outline when seen longitudinally, almost circular when viewed transversely. Below each stoma the cells are loosely packed.

4. GROUND PARENCHYMA.—This extends from the hypoderm to the centre or, as in some wheats, to the margins of the hollow pith. The cells are polygonal or

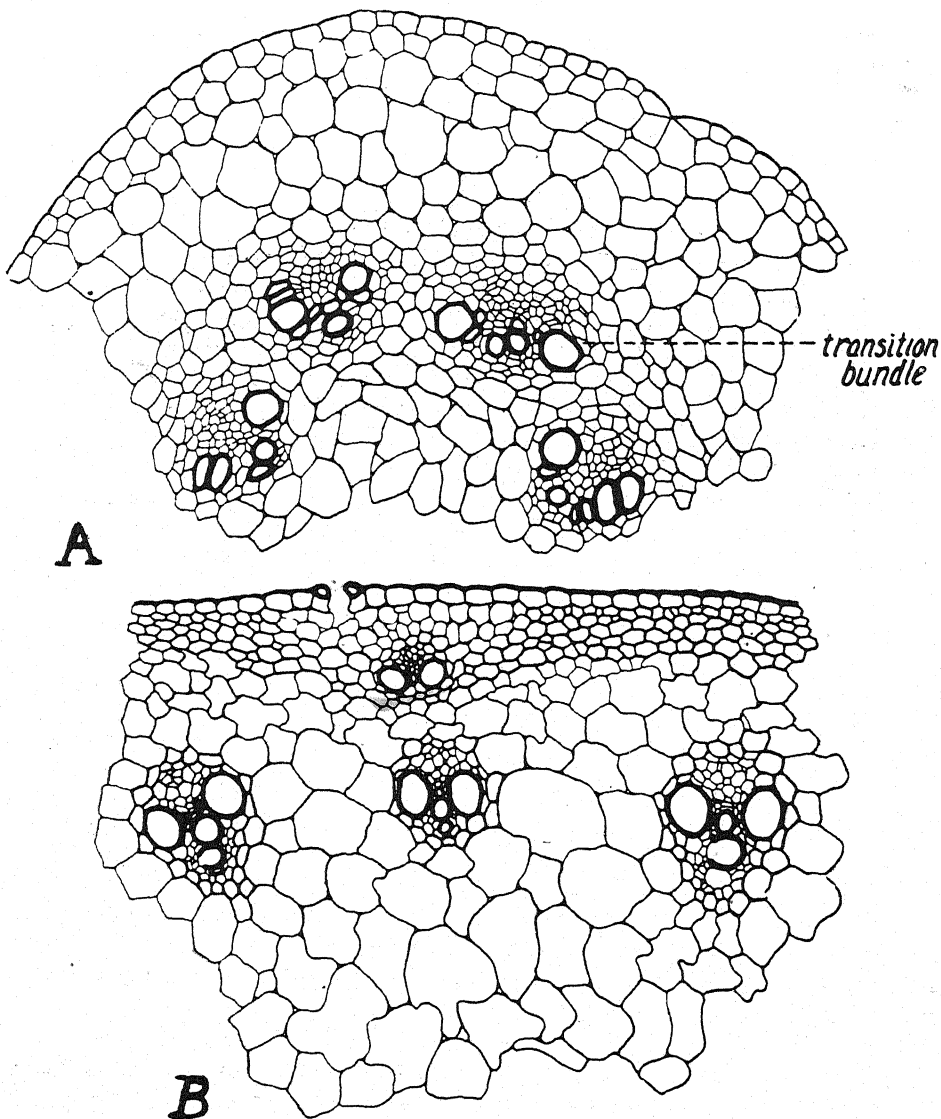


FIG. 32.

- A. Transverse section of second inter-node of six-weeks-old plant, showing transition bundles.
- B. Transverse section of portion of sixth inter-node of mature plant. (After Avery.)

rounded, the walls thin and finely pitted. At the lower inter-nodes, they may become thickened and lignified.

5. VASCULAR BUNDLES.—(a) Within the hypoderm, a ring of small bundles is to be found, alternating with the bands of assimilating tissue. (b) Nearer the centre and embedded in the ground tissue a more or less regular ring or rings of larger bundles occur.

Each bundle is of the closed collateral type. The xylem is directed towards the centre, the main vessels arranged in the form of a V. The proto-xylem lies at the apex of the V and consists of one or two annular or spiral vessels. On each limb of the V, a large pitted vessel occurs. Between the main vessels, small

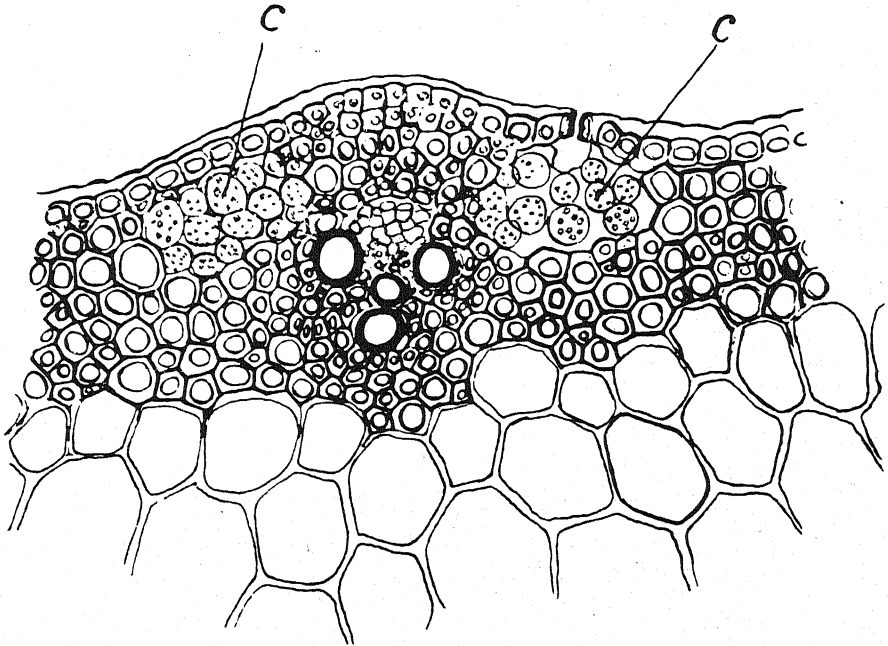


FIG. 33.

Mature stem: transverse section showing hypoderm and vascular bundle (X 380).  
c, bands of chlorophyllous tissue. (After Percival, *The Wheat Plant*, by special permission of the author.)

tracheids are to be found. The phloem occurs to the exterior, between and beyond the open limbs of the V. It is composed of sieve-tubes with their companion cells. Each bundle is surrounded by a somewhat badly defined sheath of fibrous stereome. (Fig. 34.) (Percival, 1921.)

LEAVES.—Five forms of the leaf exist. Of these, the scutellum—interpreted by many as the cotyledon or seed-leaf—and the coleoptile will be discussed in connection with the grain and the seedling. The glumes are the modified leaves of the inflorescence and will be described in the following section. There remain for treatment here the foliage leaves and the so-called prophylls, the first leaves of the lateral axes.

FOLIAGE LEAVES.—The normal leaf of a wheat as in all grasses is divisible into

two parts, the sheath and the blade. It also possesses two accessory structures, the ligule and the auricles.

1. *Leaf sheath*.—The sheath is inserted on the node and encircles the stem. For some 3 to 5 mm. above the insertion, it is considerably thickened. It is this thickening of the sheath which makes the node itself appear thickened from the exterior. Near the base the sheath is entire; higher up it is split. It is generally

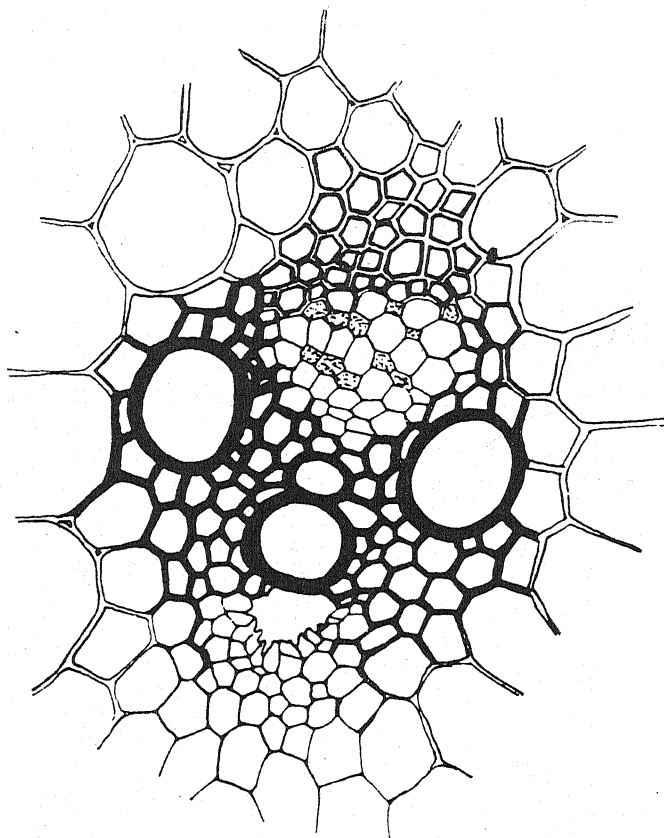


FIG. 34.

Stem Structure: transverse section of large bundle of mature stem (X 260). (After Percival, *The Wheat Plant*, by special permission of the author.)

thicker than the blade with thin transparent margins. The surface is either glabrous or covered more or less evenly with deflexed hairs. In the young plant, the sheaths are very short though the corresponding blades may have reached several inches in length. With the elongation of the inter-nodes, the sheaths rapidly elongate but are never of great length.

2. *Blade*.—The blade is long and narrow with prominent parallel veins. The tip is acuminate and slightly hooded, except in the case of the first leaf and to a less extent in the case of the second, where the tip is somewhat stiff and blunt. In older leaves, a short distance from the tip, there is a curious break in the

tissue which gives a jointed appearance to the last 1 to  $1\frac{1}{2}$  inches. The mid-rib projects on the back, and the upper surface is ribbed, the ribs often carrying hairs of varying types. The two halves of the leaf are unequal, one side being longer and narrower than the other. This side alternates in successive leaves. There is also a tendency for the whole leaf to be slightly twisted.

3. *Ligule*.—Attached to the junction of the blade and the sheath a thin membrane, the ligule, encircles the stem. It is colourless and its free margin is irregularly cut and fringed with minute hairs. The size is dependent on the age,

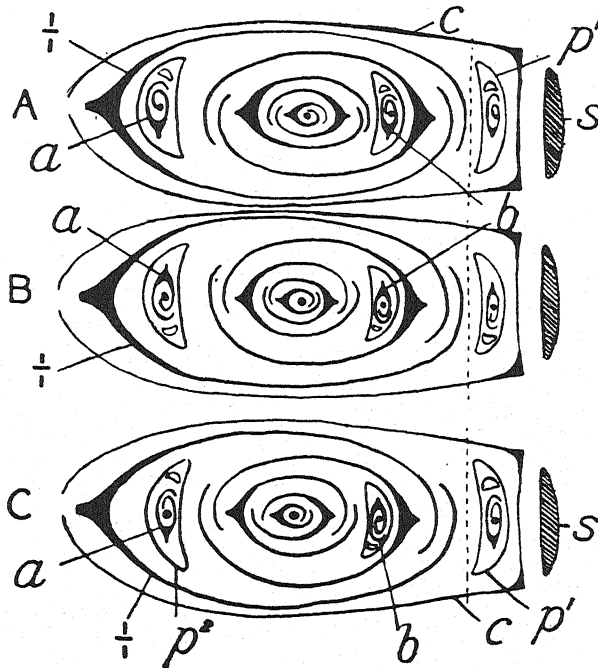


FIG. 35.

Diagram of three types of leaf arrangement, A, B and C in young primary shoots. S, scutellum; C, coleoptile;  $1/1$  first foliage leaf;  $p^1 p^2$ , prophylls of first and second laterals; a, first foliage leaf of shoot in axil of leaf  $1/1$ ; b, first foliage leaf of shoot in axil of second leaf  $2/1$ . (After Percival, *The Wheat Plant*, by special permission of the author.)

older leaves having ligules of from 3 to 4 mm. The ligule is generally regarded as a protective structure, preventing rain, dust, insects, etc., from entering and accumulating within the sheath.

In all the wheat groups, non-ligulate types are now known. As in rye and maize, they appear to have originated as recessive mutations. Barulina (1933), in a study of the inheritance of the ligule in *vulgare*, *compactum* and *durum* wheats found that the ligulate condition was always dominant, but showed a 3 : 1 segregation in the *durum* group ( $n = 14$ ) and a 15 : 1 segregation in the *vulgare* group ( $n = 21$ ). The apparent difference in the number of factors may be due to polyploidy.

4. *Auricles*.—Two claw-like appendages, attached to the base of the leaf and closely clasping the stem, constitute the auricles. Their size varies with the age and the variety. They are pale-green or pinkish in colour, their margins and tips usually fringed with long unicellular hairs.

The foliage leaves are opposite in arrangement, the divergence being  $180^\circ$ . In the lateral axes, however, the first foliage leaf has a divergence of only  $90^\circ$  from the prophyll, whilst the subsequent leaves have the normal divergence. It follows that the leaves of each axis are arranged in a plane at right angles to the plane of the leaves of the previous axis.

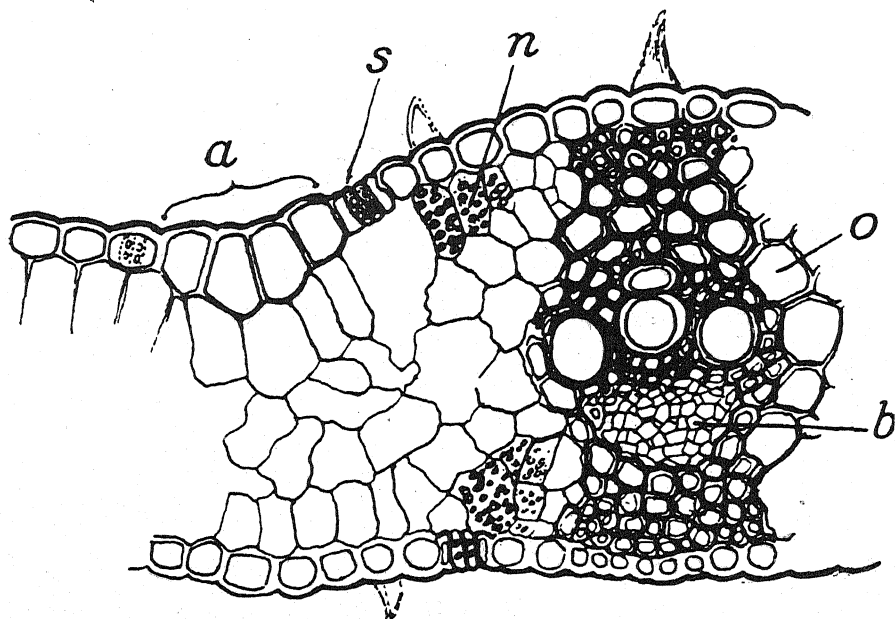


FIG. 36.

Transverse section of a leaf through a large vascular bundle (X 210). *a*, Motor cells; *s*, stoma; *n*, mesophyll cells; *b*, phloem of vascular bundle; *o*, outer sheath of bundle. (After Percival, *The Wheat Plant*, by special permission of the author.)

In the buds the leaves are convolute, the right margin being folded over the left or vice versa. This alternates from leaf to leaf. The first leaf, however, is rolled either to the right or to the left.

**PROPHYLLS.**—This term is applied to the first leaf of the lateral branch or tiller. It somewhat resembles the coleoptile, being a 2-nerved semi-cylindrical sheath-like structure with an opening at the apex, through which the first foliage leaf emerges. It grows until it is about an inch in length and then splits away from the axis. Thereafter it tends to wither.

**ANATOMY OF THE LEAF.**—The wheat leaf is composed of four tissues—the epidermis, the assimilating parenchyma, the strengthening tissue and the vascular bundles.

**EPIDERMIS.**—The epidermis forms a continuous covering to the leaf except where it is broken by the stomata. The majority of the cells are elongated and associated end to end in parallel series. Some of these series consist wholly of such cells. In other series, short square cells are here and there intercalated. The stomata usually occur in definite lines, long cells alternating with stomata.

The lower surface is flat, the cells being somewhat similar throughout with the stomata in parallel bands. The upper surface is ridged and the cells show a greater diversity. On the top of a ridge, the cells are elongated, thick-walled and pitted, often alternating with hairs. Between each ridge the cells vary. On the

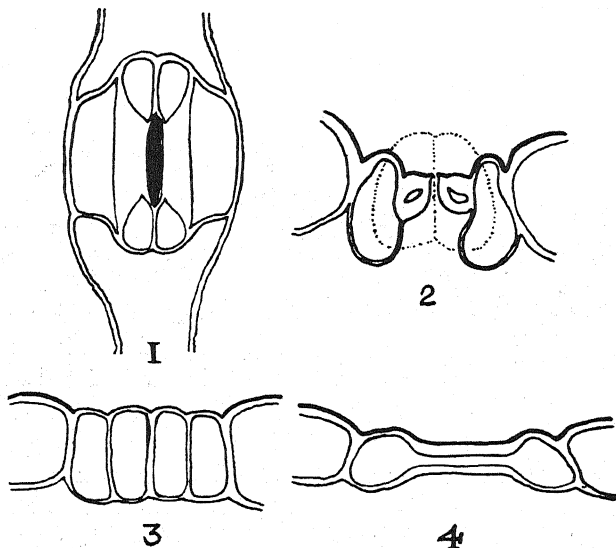


FIG. 37.

1, Stoma, surface view ; 2, median transverse section ; 3, transverse section across one end ; 4, longitudinal section of a guard cell (X380). (After Percival, *The Wheat Plant*, by special permission of the author.)

flanks, two to three rows of elongated cells occur. Parallel to and below these cells, single or double rows of stomata follow. In the furrow are to be found the "motor-cells"—3 to 7 rows of elongated cells with comparatively thin walls and greater internal than external width. (Fig. 36.)

On the leaf margins, the epidermal cells have specially thick sinuous walls.

The epidermis of the sheath is somewhat modified. The cells are in rows, elongated as in the above, their walls sinuous and much thickened. At the base the cells become shorter, and at fairly regular intervals in the rows, pairs of cells—the upper oval, the lower broader and curved—are interspersed.

**Stomata.**—The stomata are slightly sunken below the surface, in single or double rows. The single row is the usual type on the lower surface. On the upper surface, the rows, single or double, are adjacent on one side to the motor-cells.

Each stoma consists of four cells—two narrow elongated guard cells with two

small sister guard cells at either end. The two ends of the guard cells are thin-walled and united on one side to the wall of the sister cell. The wall of the middle portion bordering the pore is nearly uniformly thickened. (Fig. 37.)

The number of stomata on the upper side is greater than on the lower, the ratio being on the average 10 : 7. (Percival, 1921.)

**LEAF PARENCHYMA.**—The greater part of the parenchyma consists of assimilating tissue with lenticular chloroplasts. The outer cells, both above and below, are somewhat elongated and more or less regularly arranged, their long axes at right angles to the surface. Within, the central tissue consists of more irregular loosely packed cells. The true assimilating tissue with abundant chloroplasts is arranged in parallel strips between the bundles. It extends from the upper epidermis inwards in a layer some 3 to 4 cells deep. The rest of the parenchyma on the inside of the bundles and next the lower epidermis is colourless.

**LEAF VASCULAR BUNDLES.**—Three types of vascular bundles are to be found. (a) The major bundles, (b) the minor bundles which are more slender and generally without distinct upper girders, and (c) the transverse veins, fine, slender and crossing from one bundle to another. The total number of bundles varies from about 20 to 80. There is some division towards the base and some fusion towards the apex of the leaf.

The bundles are collateral, the xylem above and the phloem below. Each bundle has an inner and an outer sheath. The outer sheath is the more obvious, especially in the minor bundles. It consists of thin-walled cells, almost circular in transverse section, but nearly five times longer than broad when viewed longitudinally. It is interrupted on the lower side, and in the major bundles united to the "girders." It contains few or no chloroplasts. The inner sheath is continuous and composed of elongated thick-walled cells with square ends and a few simple pits. (Fig. 36.)

In the major bundles there are usually two large vessels in the middle, with annular or spiral thickenings, and on either side, two large vessels with wider bore and elliptical pits.

In the minor bundles, vessels are usually absent.

The remainder of the bundle tissue is similar to that of the stem bundle. The anastomosing veins consist of short tracheids with parallel thin-walled parenchyma cells.

• **SCLERENCHYMA.**—Above and below the bundles, and running parallel with them along the leaf, strands of sclerenchymatous fibres occur, their walls so thickened that the lumen is almost obliterated.

In the major bundles, this tissue is well-developed and "girders" the bundle to the epidermis both above and below. In the minor bundles, the sclerenchyma is less obvious, usually consisting of small isolated strands above and below the bundles and just within the upper and lower epidermis, the tissue between being filled by thin-walled tissue.

In the leaf sheath, the bundles are girdered to the epidermis with sclerenchyma continuous with the lower sclerenchyma of the blade. As it passes downwards, it increases, until about the node it becomes free from the epidermis, forming a strong strand—semi-elliptical in section—on the outer face of each bundle.

Along the margins of the leaf blade but not of the leaf sheath, there is a stout

band of thickened tissue, 80 to 100 $\mu$  wide, immediately below the epidermis. (Percival, 1921.)

**INFLORESCENCE.**—The inflorescence of the wheat is the so-called “ear”—a compound distichous spike, whose primary axis bears two opposite rows of lateral spikelets and a single terminal spikelet. In *Triticum monococcum*, the terminal spikelet is rudimentary or absent; in all others, it is potentially fertile.

The initial of the inflorescence can be seen in the seedling, but the ear does not escape from the enveloping leaf sheaths until some 4 to 6 weeks later.

The main axis consists of a number of short inter-nodes. Each inter-node is narrow at the base and broader at the apex; one side is more or less convex, the other flattened or concave. The position of the concave side alternates, so that the whole axis has a zig-zag appearance. The lateral edges are fringed with hairs of varying length. The spikelets are sessile and arranged alternately, the insertion being at the apex of an inter-node. The broadside of the spikelet is next the concave surface of the axis.

The length of the inter-nodes varies. In some types, the inter-nodes are very short, producing a “dense ear,” whose spikelets project at first at a fairly wide angle; in others, the inter-nodes are long, producing a “lax ear” with spikelets pressed against the axis; intermediate types also occur.

In the majority of wheats, the axis is tough and does not break even when thrashed. In certain others (*Triticum aegilopoides*, *T. monococcum*, *T. dicoccoides*, *T. dicoccum* and *T. spelta*), the axis is brittle and disarticulates at each node or breaks transversely when ripe, either above or below the spikelets. On thrashing, the grains of these wheats tend to remain within the glumes.

**SPIKELETS.**—The spikelet consists of a shortened jointed axis, the rachilla, carrying a variable number of alternately placed solitary and sessile flowers.

At the base of each spikelet and common to the whole, two glumes occur. They appear to be opposite one another. Actually, the insertion of one is slightly above that of the other. These glumes show marked variation in different types. The typical glume is somewhat boat-shaped, the main nerve dividing it into two unequal halves of which the outer is the broader. In some, the keel extends throughout their length; in others, the keel only runs for a short distance, the base of the glume being rounded. The apex may be broad with a blunt extension of the mid-rib, or narrower with the nerve continued into an acute point; in a few, this becomes a scabrid awn 2 to 5 cm. long. The colour may be white, red or black with intermediate shades. The surface is either glabrous or more or less hairy.

The number of the flowers varies. The lower flowers are usually perfect; the upper and especially the terminal, rudimentary or absent. As a rule, two grains mature, but three grains may form in certain varieties and, very exceptionally, four.

Each flower possesses 2 bracts—a lemma and a palea. They are situated almost opposite one another, the insertion of the lemma being below that of the palea.

**LEMMA.**—The lemma is more or less boat-shaped, with several nerves but no distinct keel. The upper margin is notched and ends in a point or awn. If the apical point does not exceed 1 cm., the wheat is said to be “beardless”; if it



exceeds 1 cm., the wheat is said to be awned or "bearded." When present the awn is tapering and somewhat four-sided with scabrid forwardly pointing teeth running along the angles. The colour of the lemma varies from white to red and black. The awns may be of the same colour as the lemma or different, *e.g.*, black awns may be found on white, red or black lemmas. The claim has been advanced that there is a relation between the awned condition and yield. Maskalenko (1929), however, was unable to find any relation between the presence of awns and the yielding capacity, a conclusion which has since been corroborated by the more recent work of Aamodt and Torrie (1934). (But see the positive relationship claimed to exist in barley—pages 247-249.)

**PALEA.**—The palea is a thin membranous bract opposite the lemma. It is symmetrical and somewhat slipper-shaped, with two prominent lateral nerves at the angles.

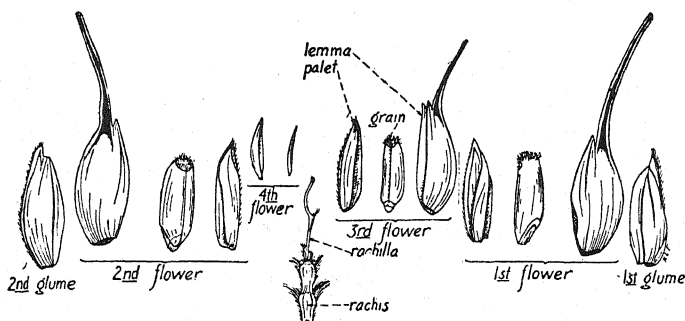


FIG. 38. Spikelet of wheat dissected, the parts removed in order. (After Robbins, *Botany of Crop Plants*, by special permission of P. Blakistons, Son and Co., Inc.)

**STRUCTURE OF THE FLOWER.**—*Perianth.*—Two lateral scales opposite the palea are generally interpreted as being the perianth segments. They are thin and colourless, narrow at the base, then expanding and again narrowing. The upper margin carries long hairs. At flower opening, they swell and become more or less spherical and pellucid. The glumes are thus forced apart and the stamens and stigmas allowed to protrude. Thereafter the lodicules shrivel and collapse.

*Androecium.*—The stamens are three in number. Their filaments are slender and attached to the anther lobes about 1 cm. from the base of the lobe. Before flowering the filaments are short; just before the flower opens the filaments lengthen rapidly.

The anthers are bi-lobed and versatile, at first green in colour, becoming later yellow or pink. Each lobe has two loculi, the tissue between each loculus breaking down before dehiscence. The pollen grains are smooth and spherical or slightly oval. In the exine there is a circular or oval pore closed by a minute lid, which is pushed off on germination.

*Gynaeceum.*—There is a single median carpel. Its basal ovary is obovate or obconical and slightly triangular in section. The sides are smooth but the broad apex has finely pointed unicellular hairs. From the tip arise two terminal styles 3 to 4 mm. long. Each is composed of a central tapering column with from 80 to 100 delicate stigmatic branches. These extend to the base on the inner side but on

the outer side are limited to the upper third. Each branch is composed of four rows of elongated cells, the upper end of each cell being free and curving outwards into a bluntish point.

The ovary wall is about 0.35 mm. thick. It has a well-defined outer epidermis; a middle parenchyma of from 8 to 14 cell layers; and an inner epidermis which is like the outer but thinner. Two lateral fibro-vascular bundles and one dorsal bundle run from base to apex.

*Ovule*.—Attached to the inner ventral face of the chamber of the ovary by a broad placenta is the <sup>ovule</sup>ovary. It has two integuments, an outer and an inner, both consisting of a double layer of cells. The inner integument arches over the whole surface leaving the micropyle free. The outer is incomplete and does not reach the micropyle.

The ovule consists of a mass of parenchymatous tissue—the nucellus—whose epidermis of closely-fitting cells is well-defined.

At a fairly early stage in the development of the nucellus, a single cell at the apex just below the epidermis enlarges and functions as the megaspore mother cell. This cell divides by a periclinal wall into two and then again into four. The three outer cells collapse but the fourth enlarges and comes into contact with the epidermis. It is the functional megaspore and enlarges to become the embryo-sac. (Percival, 1921.)

The development of the embryo-sac appears to be normal. It increases in size and at maturity has absorbed a considerable part of the nucellus. Its single nucleus divides three times and so gives rise to the 8 primary nuclei of the sac. These orientate themselves as follows. At the micropylar end, 3 nuclei form the synergidae with the ovum below and slightly to one side; other two nuclei migrate towards the centre until they meet. Fusion, however, is delayed until fertilization. The remaining 3 nuclei form at the lower end the 3 primary antipodal cells. These increase in size at the expense of the nucellus, producing a convex mass of cells on the placental side of the sac near the chalaza. The number at fertilization is from 6 to 10 though more than 36 have been reported (Körnicke, 1896). After fertilization, the antipodals gradually disintegrate.

**FLOWER OPENING AND POLLINATION**.—The opening of the flowers takes place some days after the escape of the ear from the sheath.

The first ear to flower is that of the primary culm, followed by those of the laterals in order of origin. In any one ear, the first spikelet to flower is situated about two-thirds of the length of the ear from the base. Anthesis then proceeds upwards and downwards from this point. The last spikelets to open are those of the apex and the base. In each spikelet, the basal flower opens first and the others in succession upwards.

Flowering occurs during the whole of the day, though several authors have noted periods of maximum blooming (Gitkova, 1914; Leighty and Hutcheson, 1919). The whole ear takes from 3 to 5 days to complete its flowering. There is, however, considerable variation in the time of flowering, temperature and humidity being the most important controlling factors.

The mechanism of opening is associated with the lodicules. These swell, pushing apart the lemma and palea at times so rapidly that the flower may be fully open within twenty minutes.

As the bracts separate, the styles curve away from one another and the stigmas spread outwards. The filaments of the stamens at the same time elongate, increasing in length from an average of 2 to 3 mm. to 7 to 10 mm. in 2 to 4 minutes. As a consequence, the anthers protrude, though in some types the anthers are nearly always retained. The pollen-sacs commence dehiscence when the filaments begin to lengthen. Much pollen is therefore shed within the flower and as a rule self-pollination results.

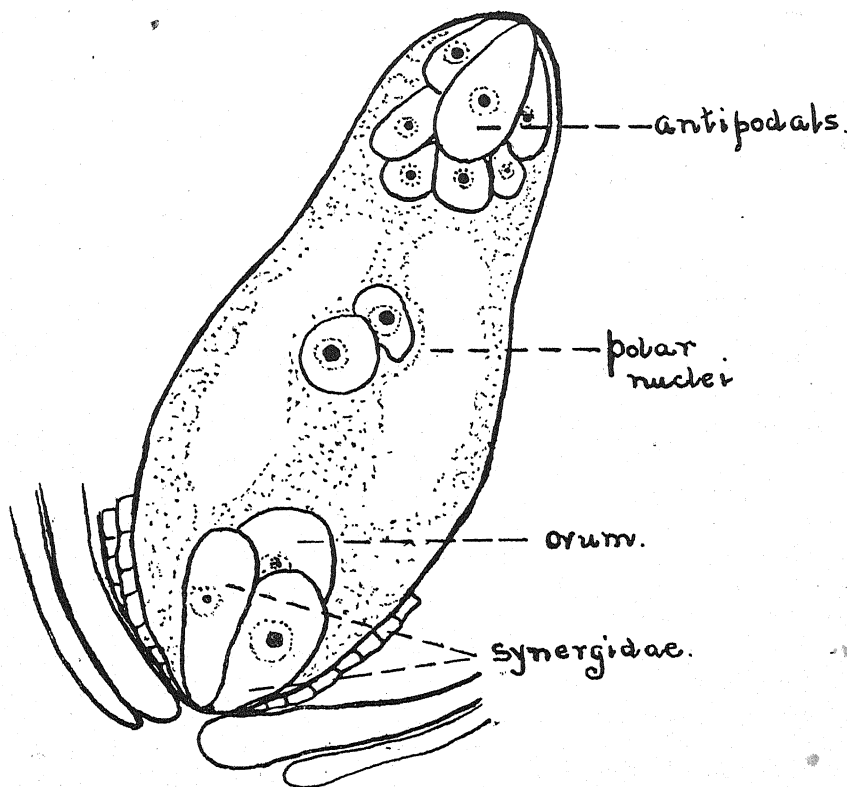


FIG. 39. L. section of embryo-sac of wheat prior to fertilization.

**STERILE SPIKELETS AND NATURAL CROSSING.**—The lowest spikelets of an ear are often sterile, especially the first three or four; occasionally one or two of the apical may also be sterile. Under certain conditions general sterility of florets may occur. Thus Salmon (1914) reported marked sterility in durum and spring wheats under very dry conditions. Obermayer found varieties in Austria which had degenerated anthers or produced scanty pollen. Pye (1918) in Australia and Shitkova in Russia report cases of sterility due to similar causes. Cahn (1925) found that there exists a difference in the amount of pollen produced in different varieties, and that under adverse conditions some may be nearly sterile. Theron has found marked sterility in certain varieties in South Africa tentatively attributed to Boron deficiency.

Nilsson-Ehle (1915) reported that the highest percentage of natural hybrids

found in any wheat variety was 0.9 per cent. Hayes (1918), and Hayes and Garber found 2 to 3 per cent. of natural crossing at Minnesota. Howard and Howard (1909), state that natural cross-fertilization is common in the Punjab, where all wheat is grown under irrigation but exceedingly rare in non-irrigated areas. This they attribute to the dry hot climate of the Punjab. Leighty and Taylor (1927) at the Arlington Station found natural crossing frequent in certain years. In some varieties the percentage was low; in a strain of Fulcaster in 1917, it was as high as 34 per cent. Percival states that 5 to 6 natural hybrids are found each year at Reading, where more than 1,500 varieties are grown annually.

In partially sterile wheat hybrids natural crossing may be high. Hayes (1918), Parker and Kurtzweil (1927) found that 18.5 per cent. of the  $F_3$  generation of certain crosses between *T. durum* and *T. vulgare* were natural hybrids.

Natural hybrids between wheat and rye have also been reported. Thus Meister (1921) in Russia found that 20 per cent. of the plants in certain winter wheat plots were wheat-rye hybrids and Leighty and Sando in 1926 reported the occurrence of 18 per cent. of wheat-rye hybrids in a Chinese variety. Even more striking is Papova's finding of hundreds of natural hybrids between *Aegilops* and wheat in Turkestan (1923).

**FERTILIZATION.**—Percival states that he has never succeeded in germinating the pollen artificially. After natural pollination, however, pollen tubes appear within  $1\frac{1}{2}$  to 2 hours, and proceed to grow rapidly downwards through the tissue of the style. On reaching the cavity of the ovary, the tube passes to the micropyle and finally comes into contact with the egg-apparatus.

Before germination, the pollen grain contains 3 nuclei, the tube nucleus and the 2 male nuclei or gametes. On germination, the tube nucleus lags behind and at times never leaves the grain. The 2 male nuclei pass down the tube and are discharged from its opened apex into the embryo-sac.

The first of these nuclei unites with the nucleus of the egg to form the zygote or oospore. The second is believed to unite with the 2 polar nuclei, a triple fusion which produces the primary endosperm nucleus. This fusion has been observed by Sax (1928), but not by Percival, who indeed suggests that the primary endosperm nucleus may result from the fusion of the 2 polar nuclei only, the second male nucleus taking no part in the formation.\*

**DEVELOPMENT OF THE GRAIN.**—A. **EMBRYO.**—After a period of rest, the fertilized egg divides transversely into 2 cells. The basal cell forms the suspensor and undergoes little further division. The upper cell divides into two and then by a wall at right angles to both, into four. This is the initial of the embryo. Growth and further division in all directions soon produces a central core of cells enclosed in a well-marked epidermis. It then becomes club-shaped with a narrow elongated base. Below the apex and on the side opposite the endosperm, a notch forms. The distal portion of the embryo above this notch develops as the scutellum.

Below the notch, the coleoptile appears as a ring of tissue, which grows up over the stem apex. As the upper half of the ring grows more rapidly than the lower, it appears as a prominent scale in longitudinal section. Thereafter the first foliage

\* This possibility does not appear to have been considered in relation to the effect of the chromosome numbers on the development of the endosperm.

leaf arises and the remaining leaves of the plumule in serial succession. After the first foliage leaf has appeared, the epiblast begins to form just below the outer base of the coleoptile.

The base of the scutellum then elongates, lifting the upper part away from the plumule. This elongated region Percival regards as the sheath of the cotyledon; the terminal portion he regards as the blade; a short overhanging portion which now forms at the top of the sheath, he interprets as the ligule ("ventral scale").

When the development of the scutellum has reached this stage, the cells of the back differentiate as the epithelial layer.

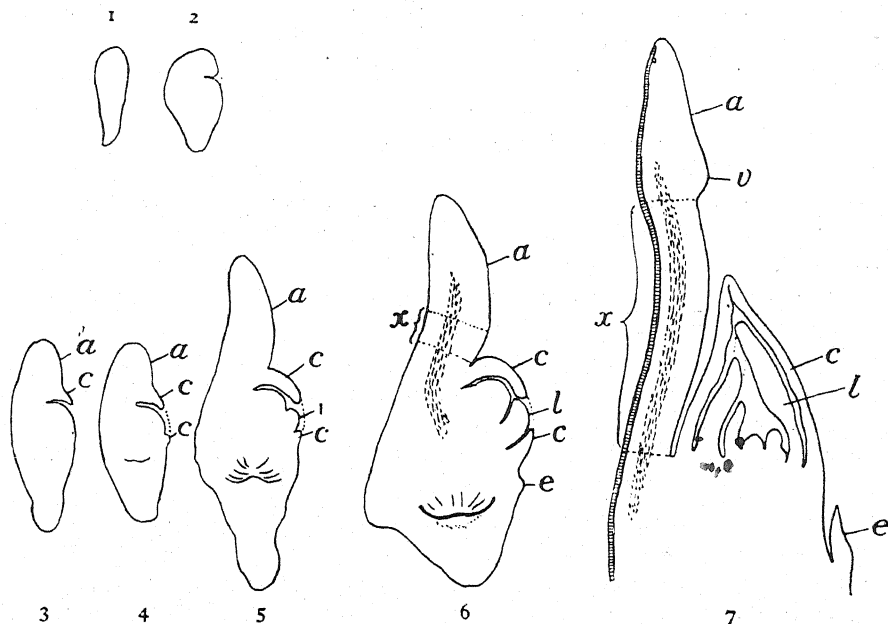


FIG. 40.

Longitudinal section of embryos in different stages of development (X 50). *a*, Upper portion of the scutellum (blade of the cotyledon); *x*, intercalary zone of scutellum (sheath of the cotyledon); *v*, "ventral" scale (ligule of the cotyledon); *c*, coleoptile; *l*, first foliage leaf; *e*, epiblast.

Length of embryos, 1, .25 mm.; 2, .25 mm.; 3 and 4, about .5 mm.; 5, .9 mm.; 6, 1.1 mm.; 7, 2 mm. (After Percival, *The Wheat Plant*, by special permission of the author.)

Meantime, in the mass of the tissue constituting the lower end of the embryo, 2 or 3 cell initials commence to divide and so differentiate the root. Owing to unequal growth, a split forms in the tissue separating the basal ground tissue from the root initial. By further growth this cavity enlarges so that on maturity the lower portion of the ground tissue appears as a sheath—the coleorhiza—enclosing the root proper. (Fig. 40.)

B. ENDOSPERM.—Before the fertilized egg starts division, the fusion nucleus or endosperm nucleus commences rapid division. Soon, free nuclei are to be found scattered in the cytoplasmic lining of the embryo-sac. Eight to ten days

after pollination, a continuous layer of cells lines the sac and by centripetal growth from this marginal layer, the vacuole of the embryo-sac is finally obliterated by endosperm tissue.

When the endosperm is completely formed, storage with starch commences. The first of the starch appears at the end farthest from the embryo, but in course of time all the cells become packed with starch except the surface or aleurone layer and the layer of 2 to 3 cells next the scutellum. This layer fills later and in the final ripening process it shrinks and forms a band of crushed cells. The aleurone layer is not obvious until the grain is half-formed.

C. NUCELLUS.—As the embryo develops, the nucellus is gradually disorganized and absorbed. The epidermis of this nucellus, however, persists, its cells dividing and expanding as the embryo grows. For a time, indeed, it might be mistaken for the aleurone forming immediately below it. Later its cytoplasm degenerates, the products collecting as a thin layer in the middle of each cell and simulating a dividing wall. The radial walls are then absorbed and as the grain dries and shrinks, the tissue collapses. Its upper and lower walls crush together, forming an extremely thin hyaline layer covering the surface of the aleurone and often recognizable with difficulty.

D. GRAIN COATS.—The ripe grain is a fruit within which lies the seed. The seed wall—the testa—and the fruit wall—the pericarp—come into contact and unite inseparably. The origin of these coats must now be sought.

1. *Origin of the Testa*.—We have seen that the nucellus is originally enclosed in two integuments, an inner and an outer; each being 2 cells thick. As development proceeds, the outer integument gradually collapses and disappears. It takes no part in the formation of the testa.

The inner integument, however, remains and expands with the grain. When the milk-ripe stage is reached, the content of the cells of the outer layer slowly disappear. A cuticle—said to be semi-permeable—develops on its outer face and the cells thereafter collapse. The cells of the inner layer remain recognizable for a longer period, and within them, in yellow and red wheats, a yellowish or reddish-brown resin-like substance forms, which seems to be partially absorbed in time by the walls. As the tissue to the outside becomes more or less translucent, this layer gives the grain its characteristic tint. Later, the radial walls disappear and as the grain dries, the inner and outer walls are crushed together. There is thus formed the “testa” or seed coat, a thin reddish-brown line of double origin, the outer part, derived from the outer layer of cells, being almost colourless, the inner part, derived from the inner layer, being brownish. The process of compression is complete when the grain is mature, and is completed last at the base of the seed, and in the groove on either side of the chalazal region (Percival, 1921, Pugh *et al.*, 1932).

2. *Origin of the pericarp (Fruit wall)*.—The original wall of the ovary is from 8 to 14 cells thick, covered externally and internally by an epidermis enclosing a delicate middle parenchyma. As growth of the ovule proceeds, these tissues multiply and enlarge, and at the same time marked changes occur.

The cells of the outer epidermis enlarge and stretch longitudinally; their lateral walls develop irregular beaded thickenings, and to the exterior a cuticle forms.

The parenchyma for some 2-cell layers below the epidermis becomes thick-walled. The remaining layers enlarge for a time but thereafter get crushed and disorganized. The innermost layer of the parenchyma (the layer next to the inner epidermis) consists at first of large cylindrical cells, 5 to 6 times as long as broad, with their axes at right angles to the long axis of the grain and with distinct chloroplasts embedded in the vacuolate protoplasm. As development proceeds the cells enlarge; the walls thicken and irregular slits or pores form;

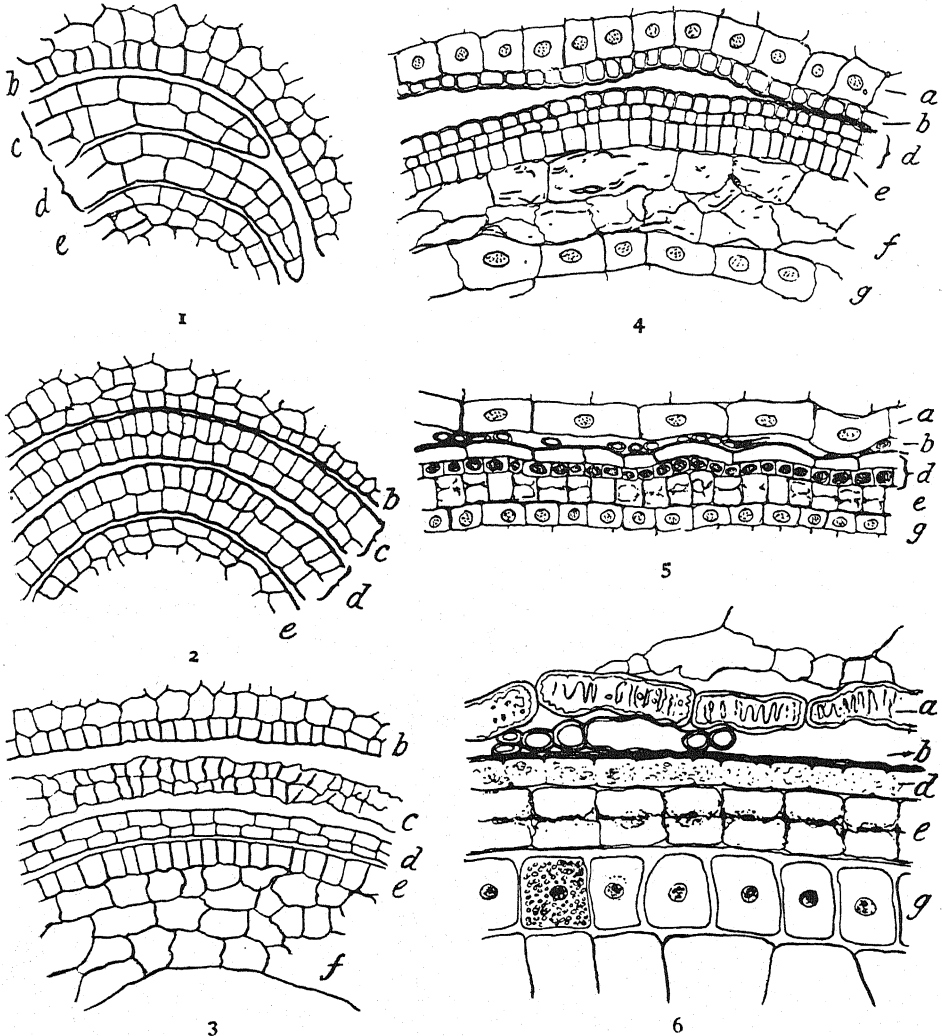


FIG. 41.

Transverse sections illustrating the changes in the inner layer of the pericarp, the integuments, and nucellus during the growth and ripening of the grain (X 270). a, "Cross layer"; b, inner epidermis of the pericarp; c, outer, d, inner integument of the ovule; e, epidermis of the nucellus; f, cells of the nucellus; g, aleuron layer. (After Percival, *The Wheat Plant*, by special permission of the author.)

the chloroplasts disappear and later all the cells shrink somewhat and become more or less bent or crumpled. At maturity they constitute the "cross cells."

The inner epidermis, at first a delicate limiting membrane composed of somewhat elongated cells parallel to the outer epidermis, shows marked change. The cells elongate, thicken to a certain extent and become isolated from one another. On the drying out of the grain they are crushed into close contact with the testa and unite thereto. They form the so-called "tube cells" of the mature grain, a layer always difficult to observe.

The relation between the final structures and the original structures may now be tabulated.

TABLE XV.  
RELATION OF OVARY AND OVULE STRUCTURE TO THE CARYOPSIS.

Ovary.		Fruit.	
Ovary Wall	Outer epidermis	Outer epidermis	} Pericarp
	Outer parenchyma	Thick-walled parenchyma	
	Middle parenchyma	Crushed cells	
	Innermost parenchyma	"Cross cells"	
	Inner epidermis	"Tube cells"	
Ovule Coats	Outer integument	Absorbed	} Seed
	Inner integument	Testa	
	Nucellar epidermis	Hyaline layer	} Seed
	Nucellus	Absorbed	
	Antipodal tissue	Absorbed	
	Primary Endosperm Nucleus	Endosperm with aleurone	
	Ovum	Embryo	

RIPENING OF THE GRAIN.—While these morphological changes are taking place, the fertilized ovary is rapidly increasing in size and form. The weight, water content and amount of dry matter also alter.

Percival gives the following figures, which indicate very clearly the changes involved.

TABLE XVI.  
RELATIVE INCREASE IN LENGTH, BREADTH AND THICKNESS. "SWAN" WHEAT  
(T. VULGARE).

(Data from Percival.)

1914.			Length.	Breadth.	Thickness.
			mm.	mm.	mm.
June	27	..	4	3	2
July	4	..	6.75	3.5	2.5
"	12	..	7	4.5	3.5
"	19	..	7	4.5	3.5
August	1	..	7.75-8	5.25	4
"	8	..	7.75-8	4.5-4.8	4
"	15 (ripe)		8.6	4.1	3.5



TABLE XVII.

RELATIVE INCREASE (OR DECREASE) IN WEIGHT, VOLUME, WATER CONTENT AND DRY MATTER.

(Data from Percival.)

L 1916.	Volume of 100 grains.	Weight of 100 grains.	Water Content.	Dry Matter.
	cc.	gr.	per cent.	per cent.
July 7 ..	3.36	2.84	70.61	29.39
„ 14 ..	4.54	4.65	68.97	31.03
„ 21 ..	5.79	6.00	60.86	39.14
„ 28 ..	6.42	7.37	52.66	47.34
Aug. 4 ..	5.86	7.66	40.75	59.25
„ 11 ..	3.95	4.86*	15.41	84.59
„ 18 ..	3.47	4.63*	11.93	88.07

\* Ripe grain from sheaves in the field.

The ripening process is a continuous one, but four stages are generally recognized.

1. Milk-ripe stage. Lower leaves dead; uppermost green. Ears green. Grain still greenish with maximum volume of water content. Endosperm with watery sap and abundant starch grains. Embryo completely differentiated.

2. Yellow-ripe stage. Leaves yellow. Ears yellow. Glumes of characteristic shade. Grains without chlorophyll; contents soft and doughy.

3. Ripe stage. The grains are hard and firm with their final tint mature; very liable to shake out of the glumes.

4. Dead ripe stage. Straw becomes dull, brittle and dirty looking. Axis of ear liable to become brittle and tending either to fall off or break in pieces. Grains very hard and falling out.

MATURE GRAIN.—The mature grain is, as we have seen in the previous section, not a seed but an indehiscent fruit with a thin-walled pericarp enclosing a single seed, whose coat—the testa—is united to the pericarp. The shape varies, but it is generally more or less oval. The dorsal surface is smooth and rounded; the ventral has a central groove or furrow, the “crease” of the millers. This furrow marks the attachment of the ovule to the ovary. At the base of the dorsal side, a small wrinkled patch indicates the position of the embryo. The apex is clothed with short, stiff hairs, curving inwards and forming the so-called brush. The colour is either red or white.

The so-called “cheeks” on either side of this crease may be round and plump, flat, sunken with sharp edges or protruded.

Boshnakian (1918), in an analysis of the factors influencing the shape of the grain, emphasizes the fact that symmetrical grains in wheat are rare. In most cases the two halves of a grain are asymmetrical, due to a flattening of either the left or the right side. This flattening is always on the side of the grain next the rachis. Consequently, all grains flattened on the left side must have been developed within the florets on the left side of a spikelet, and those flattened on

the right within the florets of the right side of a spikelet. The degree of flattening varies. It is less pronounced in *T. vulgare* than in the others. Boshnakian ranks the series as follows :—*T. vulgare* < *T. capitatum* < *T. Compactum* < *T. polonicum* < *T. turgidum* < *T. durum* < *T. spelta* < *T. dicoccoides* < *T. dicoccum* < *T. monococcum*.

The degree of the flattening appears to be due mainly to pressure caused by the tightness of the glumes.

As regards the shape of the cheeks the open spikelets of many vulgare wheats permit the development of grains with plump round cheeks. When two kernels are present and the glumes are tight, the two faces are pressed together and the cheeks are flat. If three grains are present in such spikelets the shape of the central grain depends on the size and position of the outer grains. When the grain is small, the outer grains mould themselves on the central. When it is large, the two grains whose ventral faces oppose, tend to become flattened, whilst the remaining grain situated opposite the dorsal face of the central grain develops a depression along the crease and the cheek edges become sharp.

The chief mechanical factors are accordingly :—(1) stiffness of the glumes, (2) size and shape of the area within the lemma and the palea, (3) number of grains in the spikelet and their position, (4) density of the ear, (5) pressures produced by the growth of the various parts, (6) species concerned.

Four structures are recognizable in the grain :—(1) the grain coats, (2) the nucellar epidermis, (3) the endosperm and (4) the embryo.

I. GRAIN COATS.—The origin and to a considerable extent the structure of the grain coats have already been considered in tracing their development. Some recapitulation and amplification, however, are desirable.

A. *Pericarp*.—The pericarp, constituting the major portion of the grain coats, is derived from the ovary wall. It is divisible into several layers.

- a. **Epidermis**.—This is a continuous layer of elongated cells, the walls thickened, perforated with pores, and strongly cuticularized on the exterior surfaces.
- b. **Outer parenchyma**.—Several layers of cells, the outer thick-walled and lignified, the inner thin-walled, somewhat crushed and often disorganized.
- c. **Cross Cells**.—These are generally conspicuous and consist of a single layer of elongated cells, their longest diameters at right-angles to those of the epidermis. The walls are thickened, the inner walls being thicker than the outer. Irregular slits or pores are present. Owing to pressure on the drying out of the grain, they may become more or less bent.
- d. **Tube cells (inner epidermis)**.—At first a continuous layer, the elements of the inner epidermis become separated from one another or joined at irregular intervals. The cells are hypha-like and run parallel to the outer epidermis, hence traversing the cross cells more or less at right angles. Owing to the fact that they tend to be isolated, they are difficult to distinguish in transverse section.

B. *Testa*.—This is the product of the second integument. It consists of two layers of cells crossing one another at an acute angle. The walls are thin and slightly lignified; the outer layer markedly crushed and colourless; the inner

layer less obviously crushed, its walls tinted either red or brown. (Percival, 1921.) It is to the pigment in this layer that the grain owes its characteristic colour.

On the inner side of the testa, there is a very thin colourless membrane, and on the outer a much thicker membrane. Most authors (Percival, 1921; Eckerson, 1917; Braun, 1924; Pugh *et al.*, 1932) consider that this layer is impregnated with cutin or suberin-like substances. Brown (1931), however, from observations on other material, considers that it is more highly impregnated with fat than is the case in leaf cuticle.

The outer layer of the testa is not uniform in thickness. It is thinnest over the embryo. On the dorsal side, it increases gradually in thickness up to the brush end. The thickest parts occur in the groove, along the top of the grain where it passes beneath the position of the style and in the region extending from the micropyle to the base of the groove (Pugh *et al.* l.c.).

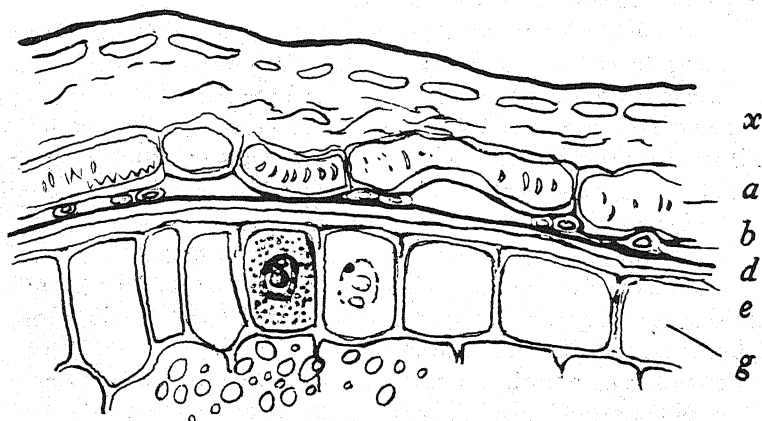


FIG. 42.

Transverse section of the pericarp and aleuron layer of a ripe grain (X 210). *x*, Epidermis; *a*, "cross layer"; *b*, "tube-cells" (inner epidermis); *d*, testa; *e*, crushed nucellar layer; *g*, aleuron layer. (After Percival, *The Wheat Plant*, by special permission of the author.)

Except at the micropyle and along the chalazal region of the groove, the testa envelops the whole seed. At the chalazal region, there is a group of cells (between the lines of origin of the testa), which possess some of the characters of the inner integument.

The grain coats together with the nucellar layer are spoken of collectively as the "bran," and constitute 8 to 9 per cent. of the grain.

II. NUCELLUS.—All that is left of the nucellus is the epidermal layer and even it may be crushed out of all recognition. It is usually detectable as a "hyaline layer," bright, colourless and without structure.

III. ENDOSPERM.—*a. Aleurone layer.*—The outermost layer of the endosperm, constituting 3 to 4 per cent. of the grain, shows marked differentiation. From the surface, the cells are polygonal with rounded corners; in transverse or longitudinal views, square or rectangular. Filling each cell is a waxy or oily cytoplasm, in which are embedded a large nucleus and numerous spherical aleurone grains.

They are not typical aleurone grains, however, as no globoid or crystalloid is present. Each consists of a thin membrane enclosing a highly refractive core. What this core consists of is by no means certain—possibly a soluble protein with magnesium and calcium phosphates.

Peklo (1913) advanced the interesting theory that the aleurone grains represent the products of symbiotic fungi present in the endosperm or in the tissues adjacent thereto. He succeeded in isolating a fungus which had the characteristics of a smut and appeared to be the same as or related to the fungus found by Freeman, living symbiotically in the grains of *Lolium temulentum*. A satisfactory method

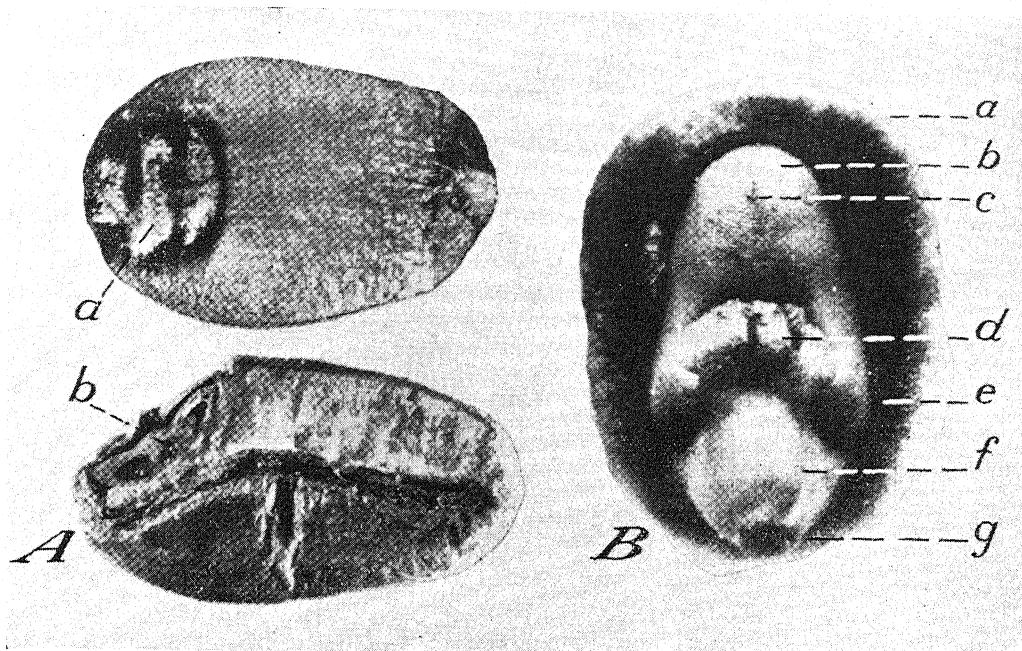


FIG. 43.

A : a, Dorsal view ; and b, sagittal section through a wheat grain, showing position of embryo. X 10. B, Face or axis view of a wheat embryo : a, Scutellum ; b, coleoptile ; c, vent of coleoptile ; d, epiblast ; e, lobe caused by lateral root ; f, coleorhiza ; g, suspensor. X 30. (After McCall.)

of growing the fungus having been secured, Jodidi and Peklo (1929) then proceeded to see whether or not it contained alcohol-soluble proteins corresponding to the characteristic proteins of the wheat aleurone layer. They claim to have established the fact that the hyphae of the symbiotic fungi isolated from wheat, barley and rye-grass contain prolamins, an essential constituent of gluten. This result supports Peklo's original statement, but the subject demands further investigation.

b. *Starch-gluten Endosperm*.—This constitutes the greater part of the grain (82 to 86 per cent.). Its cells are polyhedral and thin-walled, their long axes placed at right angles to the pericarp. They increase in size towards the

centre. Next the scutellum its cells are starchless and more or less crushed together. All the other cells contain starch granules embedded in a protoplasmic matrix. From this matrix the "gluten" is obtained. There are, however, no aleurone grains. The percentage of "gluten" is highest next the aleurone and decreases inwards.

IV. EMBRYO.—The embryo, constituting only some 6 per cent. of the grain, lies at the base of the grain on the dorsal side. It consists of a short axis with the plumule at its apex and the primary root at its base. Attached to the inner side is a fleshy shield-shaped structure, the scutellum. This forms the greater portion of the embryo. On the outer side and opposite the scutellum, there is a small tongue-like projection, the epiblast.

1. *Scutellum*.—In outline, the scutellum resembles a broad elliptical shield. It is slightly curved, the convex face pressed against the endosperm. The upper portion, beyond the point of attachment to the axis, is free and partly surrounds the coleoptile which is slightly sunk in a depression on the face. The fleshy projection situated above the coleoptile tip constitutes the ventral scale.

The epidermis of the inner face in contact with the endosperm is differentiated as the columnar epithelium. Its cells are cylindrical and elongated, their long axes at right angles to the surface of the scutellum. In some wheats the surface, especially near the upper and lower edges, may be deeply inverted to form tubular glands. The epithelium functions both as a secretory and as an absorptive layer.

The vascular system is represented by a broad strand of elongated thin-walled conducting cells which passes out almost at right angles from the hypocotyl and follows the medium plane of the scutellum to near the apex. There it widens and spreads out fan-wise in fine branches. Some of the branches end abruptly. Others curve backwards, running in fine sinuous lines almost to the base of the scutellum. It has (in *T. vulgare*) 11 bundles; the second has 7. (Fig. 168, 3 and 6.)

2. *Epiblast*.—This structure is a short, thin scale with no differentiation in its tissue, situated on the outer face of the axis, opposite to and slightly above the insertion of the scutellum.

3. *Plumule*.—The growing point at the apex of the axis is surrounded by 2 or 3 rudimentary leaves, the first of which is on the side of the axis opposite the scutellum. It has (in *T. vulgare*) 11 bundles; the second has 7.

Enclosing the plumule is a protective leaf—the plumule sheath or coleoptile, which has been variously interpreted. It develops on the same side of the axis as the scutellum. It is continuous, except at the apex, where there is a short slit on the outer face.

The first lateral bud is to be found in its axil next the scutellum. In most wheats, two large bundles occur in the coleoptile, one on either side in a plane parallel to the face of the scutellum. As many as six bundles, however, have been noted by Percival (1927), whilst Jakovlev and Nikolaenko (1931) state that many forms of *T. dicoccum*, *durum*, *turgidum* and *polonicum* (especially the Abyssinian forms) have more than 2 bundles, the commonest number being 4.

4. *Root system*.—The main root of the embryo is continuous with the tissue of the hypocotyl. Two pairs of secondary rootlets are also differentiated. They lie in a plane almost parallel to the face of the scutellum, just below the scutellar plate, and as a consequence are not visible in the normal longitudinal section. The

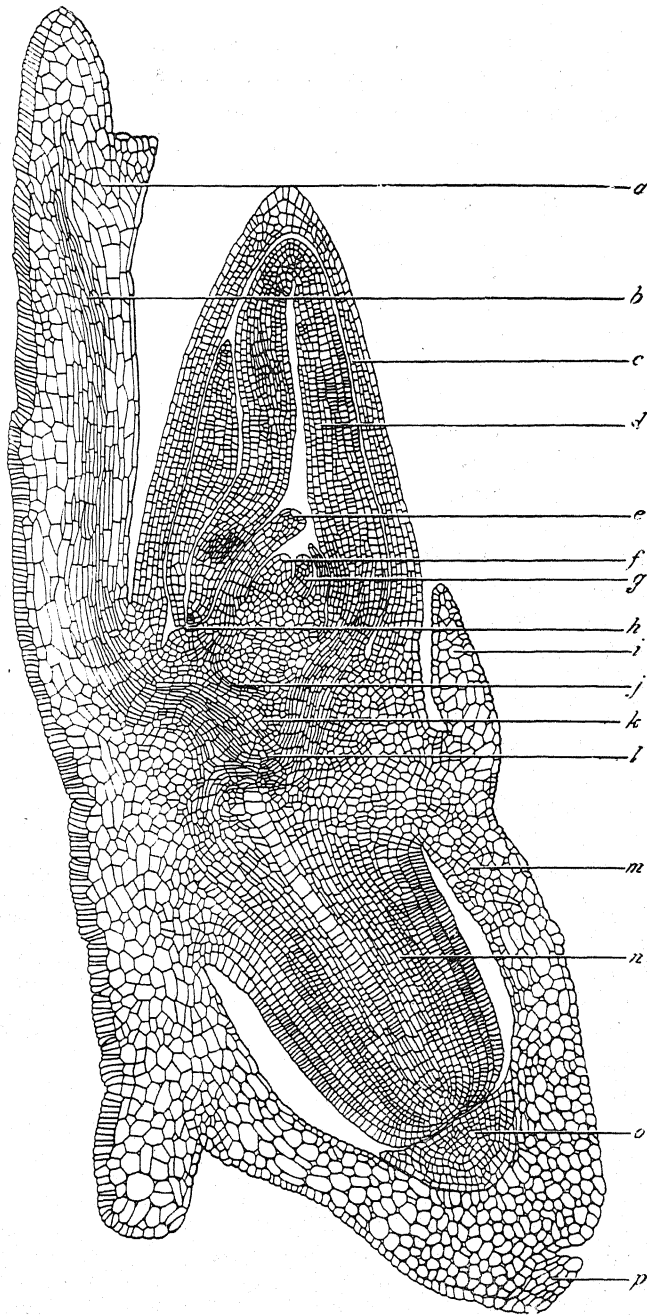


FIG. 44.

Median sagittal section of a wheat embryo (Turkey variety): *a*, Scutellum; *b*, scutellum trace; *c*, coleoptile; *d*, first foliage leaf; *e*, second foliage leaf; *f*, third foliage leaf; *g*, growing point; *h*, coleoptile axillary bud primordium; *i*, epiblast; *j*, procambium cross-axis plate, second node; *k*, first inter-node; *l*, first node, transition from root to stem; *m*, coleorhiza; *n*, primary root; *o*, root cap; *p*, remains of suspensor. X 80. (After McCall.)

first of these pairs arise at a point just above the epiblast ; the second pair develop slightly higher up. The third pair of seminal roots and the single root which forms above the epiblast in a plane at right angles to the others, are usually not differentiated in the embryo.

Each rootlet terminates in a growing point covered by a root-cap. The primary rootlet and the first pair of laterals are enclosed in the root-sheath or coleorhiza which forms by unequal growth and subsequent splitting in the basal mass of embryonic tissue. The vascular system is not clearly defined. (Fig. 44.)

*Embryo-less grains.*—Lyon (1928) reports the finding of 0·1 per cent. of embryo-less seeds in twenty different lots of samples from several varieties of wheat. On dissection, no trace whatsoever of embryo tissue could be found in these seeds. A similar condition has also been found in certain selected strains of wheat by Kamensky and Orechova (1932).

THE IDENTIFICATION OF VARIETIES IN THE GRAIN.—The issue in recent years of pure line strains of many varieties has raised many difficulties in the "certification" of grain samples. Obviously, morphological differences, however refined, can only be used for identification up to a point. Consequently, methods have been devised to supplement these morphological differences. Of these methods, the reaction of the grain to phenol has been the most widely employed. On this basis Freidberg (1933) and Voss (1935) have successfully differentiated a large number of varieties. The phenol test, however, is generally supplemented by germination tests and the subsequent behaviour of the seedlings in the greenhouse. (For a general account of laboratory methods of differentiation, see Voss *Die Unterscheidung der Weizensorten am Korn und im Laboratoriums versuch*. Mitt. Biol. Reichsanst Berlin, 1935.)\*

Freidberg (1933) further claims that the colour reactions of the grain on treatment with carbolic acid and alcoholic potash may also be employed in differentiation.

FOOD CONSTITUENTS OF THE GRAIN.—Although a wheat grain appears to be perfectly dry, there is still a considerable amount of water locked up in its tissues. The actual percentages found vary from about 9 to 16 per cent., the lower figures being found in wheats grown in hot arid climates. Some idea of the percentage of the other substances present may be gained by examining Richardson's figures :

TABLE XVIII.

## AVERAGE ANALYSES OF FOOD CONSTITUENTS.

Fat	..	2·30 per cent.	Dextrin and Sol. Starch	..	2·30 per cent.
Starch	..	67·88 per cent.	Proteins	..	11·04 per cent.
Cellulose	..	1·90 per cent.	Mineral Matter	..	1·84 per cent.
Sugars	..	3·50 per cent.	Moisture	..	9·25 per cent.

Of these substances, the fat is mainly found in the embryo and to a much less extent in the bran. The starch is almost wholly confined to the endosperm. The soluble carbohydrates (sugars) have a wider distribution, considerable quantities occurring in the embryo. Our knowledge of the proteins is probably very

\* See also (Variety testing in the laboratory), Bull. Appl. Bot. Leningrad Ser. IV (I). 1936.

imperfect. Osborne and Voorhees have demonstrated the existence of five. (1) A globulin, 0.6 to 0.7 per cent., (2) An albumin-leucosin, 0.3 to 0.4 per cent., (3) a proteose, 0.3 per cent., (4) gliadin, 4.25 per cent. and (5) glutenin, the remaining percentage. The last two constitute the so-called "gluten."

There is no "gluten" in the embryo nor in the bran. The gluten content of patent flour is therefore much higher than that of the whole grain.

The mineral constituents are high in the bran (5.7 per cent.); the finished flour has much less (0.4 per cent.). The principal constituents are magnesia, potash and phosphoric acid. As the phosphoric acid is mainly present as a phosphate, the greater part of the mineral matter is potassium phosphate.

As regards vitamin content, no vitamin C occurs in wheat. In the embryo, vitamin A and B are both found. There is, however, no vitamin A in the endosperm and only a trace of B. Both appear to occur in the bran.

It is probably due to the low vitamin content of the endosperm that white bread from patent flour is inferior to whole wheat bread in nutrition.

**GERMINATION.**—Given sufficient water, an adequate temperature and enough oxygen, the grain may germinate. Other factors are also concerned, but they are in general not limiting. The most variable factors are water supply and temperature.

The suction pressures by means of which the water passes in are of course dependent on the osmotic pressures of the cells. These pressures in most seeds are high, though it should be noted that the first entry of water must be due to imbibition by the colloids of the grain. Once in operation, the suction pressures are such that the grain is able to absorb water rapidly from soils with moderate water content. Different opinions have been held as to where and how water and solutes enter the grain. Brown (1907, 1916), working with barley, came to the conclusion that a semi-permeable membrane was there present and believed that it was associated with the "spermoderm." Shull (1913), working with *Xanthium* and other seeds, showed conclusively that semi-permeable membranes are present, attributing the semi-permeability in the case of *Xanthium* to the two innermost layers of the testa. On the other hand, Collins (1918), came to the conclusion that, in barley, the grain is invested by cuticulated membranes belonging to the testa which inhibit the entry of water except at the micropylar end of the grain. He states, "the micropyle is the point of rapid entry and the seat of differential filtration takes place along the chalazal tissue lying along the furrow." The movement is most rapid at the point "where it meets the dorsal margin of the scutellum." The observations of Pugh *et al.* (1932) on wheat support Collins' morphological observations on the barley, but they express no opinion on the permeability of the coats.

Schroeder (1911) was of the opinion that liquids penetrated the wheat grain chiefly at the embryo end and that there was a decrease in permeability from the base to the apex. This, however, was not uniform. Braun (1924) found that iodine entered over the entire surface of the grain radially but not uniformly. He accordingly concluded with Schroeder that there is a gradient of permeability and that the diffusion in the sub-aleuronic cells of the endosperm as postulated by Collins (*l.c.*) does not take place (see also Beeskow, 1924).

R. Brown (1931), however, in discussing the entry of water into the



grains of Gramineae found no evidence in support of either Collins' theory or of the assumption of a gradient of permeability. Instead, he is of the opinion that there is a semi-permeable membrane identifiable with the testa and the cuticle-like membranes on its inner and outer faces. Water enters first at the micropylar end and then diffuses into the lower end of the endosperm. The swelling of the cells that there takes place stretches the testa, which consequently becomes more permeable. Water, therefore, enters through the stretched seed coat enabling a further upward diffusion to take place, and so leading to a gradual upward spread of the area of absorption towards the apex. The increase in permeability is, therefore, due to an increase in the size of the inter-molecular spaces.

In a later paper, Brown (1932) has shown that a solution such as silver nitrate penetrated readily as far as the "cuticular membrane" of the testa. There it was arrested and tended to be deposited in a sharp line along the surface. After 40 hours it passed slowly into and accumulated within the testa, and still later passed inwards across the inner cuticle. This proceeds slowly from the 40th to the 60th hour. According to the nature of the solute, two sequences may be observed. If the membrane be freely permeable to the solute, the absorption of the solute is similar to that of water. So iodine, *e.g.*, first penetrates at the base and is then absorbed at higher and higher levels as the area of absorption of water spreads upwards. There is no accumulation of the solute in the testa. If, however, the membrane is only slightly permeable to the solute, then the sequence is as described for silver nitrate. In the first instance, the curve representing absorption is an exponential one; in the second, where there is retardation by the testa, the absorption time curve is more complex.

He concludes that the factors regulating the absorption of the solute appear to be 1/ electrical absorption in the cuticle-like membranes of the testa, 2/ mechanical absorption in the testa and the tissues of the endosperm and embryo, 3/ the inhibitional pressure developed in the endosperm, and 4/ the size of the inter-molecular spaces of the semi-permeable membranes. Each solute will re-act to the above factors according to its own particular properties.

As the water enters, the grains swell and increase in weight. The percentage increase in weight for 48 hours is from 30 to 45 per cent.; that in volume is somewhat higher.

The optimum temperature for germination is stated to be about 84°F. The minimum is about 40°F. Above the optimum grains germinate irregularly, the more irregularly the higher the temperature. In the soil and under favourable conditions, germination commences in 4 to 5 days. Differential response of varieties in speed of germination has, however, been demonstrated. (Voss, 1934.)

The first part of the embryo to appear is the coleorhiza, which swells considerably and thus tears a longitudinal slit in the coat, exposing the plumule. It then expands transversely and grows to a length of about a millimetre. The primary root then appears, having bored its way through the sheath at a point a little to one side of the apex of the sheath. The first pair of lateral rootlets appear an hour or two later. The second pair emerge in the same plane some days after and just above the first pair.

Meantime, the coleoptile is lengthening and when the grain is sown about an inch below the surface, it thrusts its spear-like point through the soil in about

ten days. In some forms, it is pale-green or nearly colourless ; in others, pink. Its length depends on the depth of planting.

Utilization of the reserve food. The epidermis of the scutellum in contact with the endosperm is, as already noted, the so-called columnar epithelium. Its cells are cylindrical, elongated at right angles to the curved surface of the scutellum, and in function are both absorptive and excretory.

As germination proceeds, its cells elongate ; their apices become swollen and separate from one another, the free ends projecting into the endosperm.

From these cells, diastase is secreted, an enzyme which renders starch soluble and diffusible. A certain amount of diastase is also produced within the aleurone layer, which also secretes a gluten transforming enzyme and cytase. It is to this cytase that the rapidity of the food transformation is due. For the cytase breaks down the cell walls of the endosperm from the outside inwards, thus enabling the other enzymes to act directly on the reserves. As a consequence, the whole mass of cells is reduced, first to a white pasty mass and then to a semi-fluid. The material thus rendered liquid is absorbed by the epithelium and transferred through the scutellum to the growing embryo.

**SEEDLING.**—When the seedling reaches the ground level it has the structures already noted. The grain is rapidly becoming a mere sac containing the diffusible food substances. The coleoptile has grown upwards and its tip projects above the ground level. The rootlets are five in number. Later, the sixth or epiblast rootlet may appear, followed in some cases by the third pair.

Near the tip of the coleoptile on the side away from the scutellum, there is a narrow slit. Through this slit the first leaf appears. It has a divergence of  $180^{\circ}$  and its blade is rolled from one margin to the other. A second and third leaf follow, with similar divergences but with the rolling of the leaf alternating, *i.e.*, if the first leaf is rolled to the right, the second leaf is rolled to the left and so on. But the rolling of the first leaf is not constant. Seedlings may be either right-handed or left-handed. In the right-handed types, the right margin is folded over the left ; in the left-handed types, the left margin folds over the right.

The appearance of the leaves is primarily due to the growth of the third inter-node, if McCall's interpretation be accepted (1934). (Fig. 18(c).) This brings the growing point to near the ground level. The buds in the axil of the fourth and fifth nodes—which have been gradually developing—now swell, and as the inter-nodes remain short, the whole axis near the ground level appears to thicken very markedly. This thickening constitutes the “crown,” whose depth below the surface is now known to be influenced by the variety and the environment (especially temperature), as well as the depth of sowing (Govorov, 1923 ; Tavčar, 1930 ; Friedberg, 1932 ; Webb and Stephens, 1936.) Some time later, the first pair of adventitious roots develop from the first node to branch, followed by the succeeding pairs from the lower nodes. These adventitious roots of the main axis are in the same plane as the paired seminal roots. The possible development of adventitious roots above the insertion of the scutellum and below the first “crown-node” has already been mentioned. The subsequent growth of the seedling has already been described.

**ANATOMY OF THE SEEDLING.**—The anatomy of the primary root has already been dealt with. That of the secondary seminal roots is similar, but there are

several large vessels in place of one and a smaller amount of parenchyma, which soon tends to become lignified.

The axis between the scutellar node and the coleoptile remains short, and is essentially a region of transition. In cases where considerable elongation has taken place, two collateral bundles can be observed. The arrangement of the xylem, phloem and parenchyma around them may be very indefinite, some xylem groups being exarch, others endarch (Avery, 1930). Pericycle and endodermis are very indistinct, and there is a single cortical bundle as in oats. (See Figs 31 and 32.)

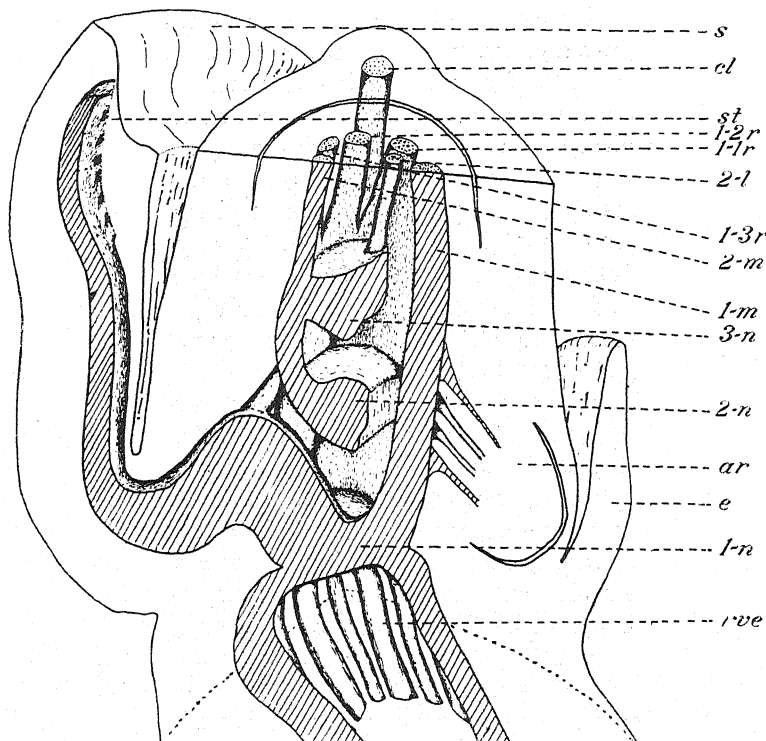


FIG. 45.

Diagrammatic perspective sagittal view of the vascular elements in the axis of a wheat seedling between the transition from root to stem and the divergence of the coleoptile. X 40. The specimen upon which the sagittal face view of this drawing is based shows somewhat more than the normal elongation in this region of the axis. Xylem and phloem of the conducting tissues are not differentiated. (Nodal plates are shown as solid structures, which is not true for that of the third node.) In the root, the strands beginning with the large strand on the posterior side are alternately xylem and phloem. The branches of the scutellum trace are not shown, except their origins: *s*, Scutellum; *cl*, coleoptile bundle (left); *st*, scutellum trace; *1-2r*, second lateral trace of first foliage leaf; *1-1r*, first lateral trace of first foliage leaf; *2-l*, lateral trace of second foliage leaf; *1-3r*, third lateral trace of first foliage leaf; *2-m*, median trace of second foliage leaf; *1-m*, median trace of first foliage leaf; *3-n*, vascular complex of third node; *2-n*, vascular complex or plate of second node; *ar*, adventitious root; *e*, epiblast; *1-n*, vascular transition from root to stem (first node); *rve*, root vascular elements. (After McCall.)

According to Avery (1930), the scutellar bundle in the axis diverges into three parts. The central part passes downwards to the scutellar plate and then turns upwards, diverging finally as the mid-rib of the leaf above the coleoptile. The two lateral parts of the original bundle pass upwards for a short distance and each again diverges. The outer of each pair becomes a coleoptile trace; the inner of each pair continues upwards, diverging finally to give rise to one or more bundles of the leaf above the coleoptile. The situation is similar to that found in the oat.

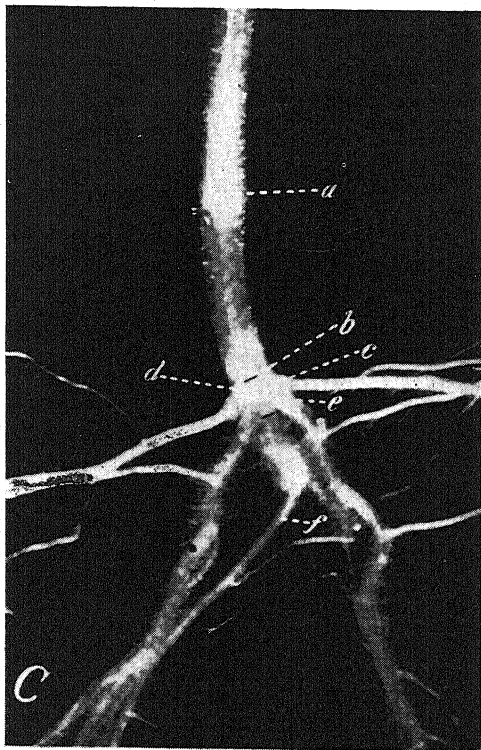


FIG. 46.

Sub-crown region of wheat seedling 14 days old. *a*, fourth node, crown node; *b*, third node, coleoptile divergence; *c*, second node, scutellum trace divergence; *d*, epiblast; *e*, first node, transition from root to stem; *f*, primary root. The upper black line marks the coleoptile divergence and the third node; the lower black line the transition from root to stem or the first node. (After McCall.)

The inter-node above the scutellum is the principal elongating region of the axis. Its bundles are not sharply defined, and there is some transition from the exarch condition to the endarch. On the whole, however, it is somewhat similar to the structure seen in the higher inter-nodes. (See Figs. 31 and 32.)

*Seedling Homologies.*—Very varied interpretations of the structures of the embryo and seedling of the Gramineae have been advanced. (See page 16.)

According to McCall (1934), the procambial plate which separates the root

from the stem in the embryo may be regarded as the first node. The epiblast is associated with this node, and may be regarded as a vestigial leaf owing to its distichous position, and its association with root origins. The fact that it has no vascular system is due, according to McCall, to its position at the first node, below which there is only root tissue.

Above the first node there is a short inter-node terminated by the second node, a cross-axis procambial plate. Immediately under this nodal plate, the scutellum trace diverges from the axis. Above the nodal plate, a pair of seminal roots originate. Because of its association with this node, the scutellum may be regarded as the second leaf, functioning as the cotyledon.

The second node is succeeded by the second inter-node, also short, and terminated by a third node. This third node is a cross-axis vascular structure, associated with the divergence of the third leaf, and above the third leaf, bud and root initials. This third leaf is the coleoptile. (Figs. 45 and 46. See also Fig. 18 (c).)

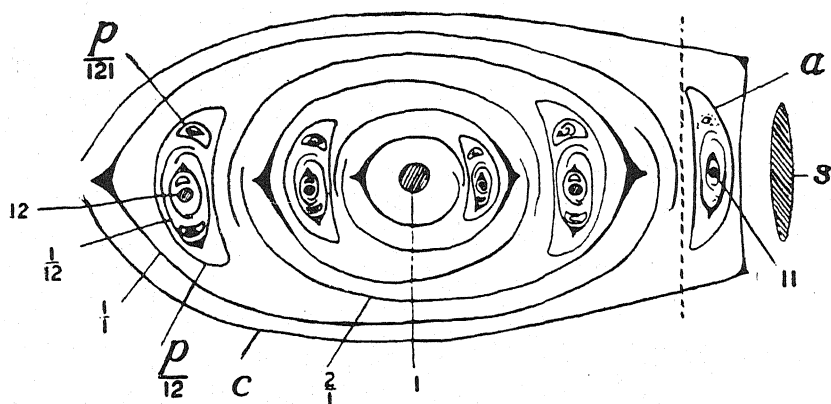


FIG. 47.

Diagram of the axes and leaf arrangements in young plant. *s*, Scutellum; *c*, coleoptile; 1, primary axis; 11, first, 12, second lateral axis of 1;  $\frac{1}{1}$ , first,  $\frac{2}{1}$  second foliage leaf of primary axis;  $\frac{1}{12}$ , prophyll of axis 12;  $\frac{1}{11}$ , first leaf of axis 12;  $\frac{2}{11}$ , prophyll of first lateral axis of axis 12. (After Percival, *The Wheat Plant*, by special permission of the author.)

McCall stresses the resemblance of the coleoptile to the prophyll, and also suggests that in origin it may be the equivalent of two leaves.

The third inter-node is at first short, but in the seedling elongates to a considerable extent. It is this region that in wheat has generally been referred to as "mesocotyl." In turn the third inter-node is terminated by the fourth node, associated with the first functional leaf (in series, the fourth leaf). This fourth node generally constitutes the first crown-node.

McCall's interpretation is simple, but is based on the belief that the procambial plate separating root from stem is the first node, the scutellar divergence the second node and the coleoptile divergence the third node. As the consequence, the region of main elongation in the seedling is the third inter-node. McCall is also exceptional in regarding the epiblast as a vestigial leaf.

Avery's interpretation, on the other hand, denies the real existence of what McCall considers node 1 and inter-node 1. The main region of elongation is accordingly node 2, above the insertion of the coleoptile. Further, the epiblast together with the ventral scale is considered as the ligule of the scutellum. (Boyd, 1931, 1932; Boyd and Avery, 1936.)

The following key by Carrier differentiates the chief seedling types :

#### DIFFERENTIATION OF SEEDLING TYPES.

1. Claws hairy.
  - A. Sheaths and blades finely pubescent, soft and velvety . . . . . Emmer, *T. dicoccum*.
  - B. Sheaths and blades not pubescent :
    1. Collar and claws large . . . . . Spelt, *T. Spelta*.
    2. Collar and claws slender . . . . . Bread Wheat, *T. vulgare*.
2. Claws not hairy.
  - A. Collar and claws large and prominent.  
Nerves of blades broad and prominent,  
upper surface smooth . . . . . Polish Wheat, *T. Polonicum*.
  - B. Collar and claws slender.  
Blades and sheaths free from hairs . . . . . Durums, *T. durum*.

Percival (1921) has emphasized the value of the nature and distribution of the leaf hairs in differentiating species. Recently Harrington (1932) has attempted to differentiate varieties of young wheat on the basis of coleoptile colour and leaf hairiness. The method within limits appears satisfactory, and might be extended.

**QUALITY IN WHEAT.**—From the farmer's standpoint, a good wheat is one which (a), gives a high yield, and (b), obtains a good price per bushel or bag. The price per bushel or bag, apart from fluctuations due to economic conditions, is in the ultimate ruled by the requirements of the miller. From the miller's standpoint, quality is determined by five factors.

1. Freedom from impurities, dirt, chaff, weed seeds, etc.
2. Freedom from certain grain diseases—in particular " smut " and " bunt."
3. The bushel weight. This should be above a certain minimum, depending in part upon the variety.
4. The percentage of water in the grain. S. African wheats average about 12 per cent. English wheats may average as high as 16 per cent. The lower the water content, the better the grain.
5. The ill-defined quality known as " strength."

**THE MEANING OF " STRENGTH " IN WHEAT.**—Strength—in relation to the manufacture of bread—may be defined as that quality in wheat which enables its flour to produce a large porous and well-piled loaf. It follows that the ultimate test for strength is the baking test. As a result of many milling and baking tests, the Wheat Committee of the National Association of British and Irish Millers adopted an arbitrary scale to give a numerical expression to the varying degrees of strength met with. The best American and Canadian wheats were graded as 100. The others were graded proportionately.

TABLE XIX.

NUMERICAL SCALE OF "STRENGTH."

Wheat.	Marks.
Canadian Manitobian No. 1. . . . .	100
U.S.A. Hard Spring Wheat No. 1. . . . .	100
Russian Ghirka . . . . .	85
London Household Flour . . . . .	80
Argentine Plate River . . . . .	80
Square Head Master . . . . .	65
Rivet Wheats . . . . .	20

On this basis, a strong wheat is one whose flour on baking produces a large, well-piled loaf. Its numerical value would be from about 75 to 100. A weak wheat is one whose flour produces a small heavy non-porous loaf. Its numerical value would be below 75. To produce a satisfactory loaf, the flour from such a wheat would have to be mixed with flour from a strong wheat. The average flour now sold is such a mixture. On the other hand, flour from weak wheats, such as Rivet, is prized for the making of biscuits.

Unfortunately, there is no standard procedure for the conduct of the baking test. Even in America where the flour used is more or less standardized, much difficulty was encountered, and the official method adopted in 1928 is still regarded as capable of improvement. In England, where the flours used are very varied, several methods have been employed, those of Humphries and Kent-Jones being the best known. Elsewhere the procedure is equally varied. As a consequence the comparison of baking tests from different countries and even from the same country is often rendered more difficult than need be.

**HARD AND SOFT WHEATS.**—In buying wheat, strength is generally judged by certain external characters. Thus, a strong wheat is generally a "hard" wheat. Most "hard" wheats are red in colour with brittle skin. The grain is almost consistently small and the endosperm hard and brittle with a horny translucent appearance. If the grains are chewed, a small pellet of gluten, tough and elastic in nature, is left in the mouth.

"Soft" wheats are in general weak wheats. The colour may be red or white; the skin is generally thick and tough; the grain is large and plump; its endosperm opaque, white, soft and mealy. If chewed, less gluten is obtained and its texture is less tough and elastic.

In estimating quality from the grain the hardness and vitreousness are perhaps the best indices. In addition, the bushel weight, the thousand grain weight and the specific gravity are generally taken into consideration. Together they constitute a useful but by no means a reliable indication of quality.

**FACTORS THAT PRODUCE "STRENGTH."**—A strong wheat has been defined as one whose flour produces a large well-piled loaf; a weak wheat as one whose flour produces a small compact loaf. Wherein lies the difference?

In the making of bread, flour is mixed with water and yeast added. The yeast feeds on the sugar in the flour and so causes a fermentation which results in the formation from the sugar of alcohol and carbon-dioxide. The dough as a consequence "rises," owing to the formation of gas bubbles. This bubble formation is due to the presence of the gluten which, tough and elastic in nature,

retains the gas. Now when the dough is placed in the oven, the heat hardens and fixes the walls of the bubbles, and we get a bread with a varying but yet characteristic porous structure. No other cereal contains this gluten and as a consequence we can only make bread from wheat flour.

Two groups of factors may be distinguished in the process. These are (1) the factors responsible for the size of a loaf, and (2) the factors responsible for its shape and texture.

1. *Size Factors*.—On mixing different samples of flour with water and adding yeast, gas is given off from all the samples at practically the same rate for the first three hours. This is due to the fact that all flours contain approximately 1 per cent. of sugar. To this initial sugar the primary fermentation is due. After the third hour, however, the gas production is not the same in all samples. In some, the gas production per hour falls off and remains low: in others, it may fall off slightly and then maintains itself at a fairly high figure. Obviously, if the gas production is not maintained the dough rises only to a limited extent, and a small loaf results. If the gas production is maintained, the dough continues to rise and a large loaf results.

Now the gas production is due to the fermentation of the sugar by the yeast. There is sufficient sugar in all flours to ensure gas production for 2 to 3 hours. Thereafter it is exhausted. Variable amounts of gas, however, continue to be produced. Where does the sugar for this fermentation come from?

There is only one possible source. We have seen that the grain contains the enzyme diastase. This diastase can convert starch into sugar. Hence the later gas production must be due to sugar produced by diastatic activity from the starch of the flour. The amount of the gas produced must then depend on the amount of the sugar produced. The amount of the sugar produced must depend on either the amount of the diastase or the activity of the diastase or both together.

The size of the loaf is, therefore, mainly due to the diastatic activity of the flour—and this can be measured. We have only to estimate the amount of gas produced per hour for a definite period of time from a known quantity of flour in a known quantity of water when activated by a known amount of yeast. (In practice, 20 cc. of yeast mixture—made from  $2\frac{1}{2}$  grams of compressed yeast in 100 cc. of water—added to 20 grams of flour and incubated at 20°C.) A strong flour under test gave 20 cc. of gas during the sixth hour; a weak wheat gave only 5 cc. during the same hour.

Some further factors as regards size should be noted. Thus temperature definitely influences the diastatic activity, the standard temperature now employed being 27°C. (*Standard Methods of the American Association of Cereal Chemists*. Lancaster Press, Lancaster, Pa., 1928.) It is also influenced by the pH of the medium, the optimum being 4.8; increases, however, have been noted at higher values (5.2). (Rumsey, 1922.) At the same time, the initial pH of wheat flours varies considerably. (Mangels, 1926; Hermano and Rask, 1926; Malloch, 1929.) There is also evidence that the starch grains themselves show variable resistance to diastatic action (Alsberg, 1927 and 1928; Malloch, 1929; Möhs, 1931), and that mechanical injury during the milling process may influence the action. (Alsberg and Griffen, 1925; Alsberg, 1927, 1928; Karacsonyi and Bailey, 1930.) In addition, flour from sprouted grain naturally has a higher diastatic power than



flour from unsprouted. (Fitz and Swanson, 1916; Sherwood and Bailey, 1926; Markley and Bailey, 1931.)

2. *Shape and Texture Factors*.—Although much work has been done on the factors influencing shape and texture, the analysis of the problem is still incomplete and part of the evidence somewhat conflicting.

There appears to be some relation between the protein content and the quality of the flour. Unfortunately, protein content varies in any one variety from year to year. Jørgenson (1930-1931) has shown that a definite minimum value (about 9 per cent. protein) must be present for good baking quality. Above this value, he was of the opinion that there is no relation between nitrogen content and quality. On the other hand, Chingo-Chingas (1931) regards the limiting value as 19 per cent. for winter wheats and 17 to 19 per cent. for spring wheats. Any further increase in protein content has no effect.

Attention was then directed to the gluten content. The total per cent. present was found to show no precise relation to the product, although a partial relationship is indicated. Gluten was then found to consist of two proteins—gliadin and glutenin. The relative proportions of these were then studied, but again were found to exhibit no precise correlation.

Gluten, however, is a colloid which is dispersed in the dough as a fine mesh-work of fibrils, in which the starch and other substances are enmeshed. Many factors, therefore, may influence its general properties.

Thus in very weak acids, gluten is dispersed. If the acid be increased in strength, the gluten begins to cohere and finally becomes tough and elastic. The acidity of wheat, however, appears to be insufficient in itself to make the gluten cohere to any marked extent.

Other factors that might influence coherence were then studied. According to Wood (1907-08), one of the main factors must be the salts present in the wheat—the chlorides, sulphates and phosphates in particular. The effect of these salts, however, is very different. Chlorides and sulphates, for example, tend to make the gluten hard and brittle. Conversely, phosphates render it tough and elastic. Now the proportions of these salts vary in different samples. Flour from a strong wheat was found to contain more phosphates than that from a weak, and at the same time very little sulphate and chloride. A weak flour, on the other hand, contained less phosphate than a strong, but was comparatively rich in chlorides and sulphates.

A generalized picture of the situation can thus be made. When the risen dough of a strong wheat is baked, the gluten, rendered tough and elastic by its particular "environment," prevents the gas bubbles from escaping. Hence the shape and also the porosity tends to be retained. On the other hand, the conditions in a dough from a weak flour renders the gluten less elastic. There is a tendency for the gas bubbles to unite and escape as the gas expands with the heat. As a consequence the shape is partly lost and the loaf tends to sink and lose porosity.

In other words, the postulate may be made that a strong flour is one whose gluten possesses good colloidal properties; a weak flour one that possesses poorer colloidal properties. These properties are not inherent as such, but are conferred upon the gluten by the "environment" which surrounds it—a complex which varies in acidity, water content, relative salt content and other factors. In any one

flour the balance of the constituents present produces an "environment" which thus confers on the gluten certain definite qualities. But what precisely the constituents are and what their proportions must be to produce "good" colloidal properties at the one extreme, and "poor" colloidal properties at the other, are at present known only in outline and by no means in detail. There are wheats which naturally possess a tendency to the one extreme or to the other, with many forms bridging the gap.

Finally, it should be noted that the baking quality generally is influenced by the age of the flour. Freshly milled flour does not bake so well as older flour. Older flours, again, may depreciate, often to a marked extent, the main factors responsible being temperature and moisture.

In breeding wheats for quality, it is of the greatest importance to obtain a satisfactory index of the baking quality from the flour or meal of a small quantity of grain. Various methods have been advocated. Pelshenke's fermentation time test (Pelshenke, 1930-1931, etc.; Cutler and Worzella, 1931); Berliner's method (employing bruised grain or flour) of estimating the swelling co-efficiency of the gluten (Berliner and Koopman, 1929); the method of testing the elasticity of the dough of Chopin (1921) and Vilmorin and Chopin (1929) and several "distension" methods; all require but small quantities of grain and have given, within limits, valuable indices.

IS STRENGTH A RACIAL OR ENVIRONMENTAL CHARACTER?—Recent experimental work has shown that the quality known as strength may be due either to environmental conditions or to inherent factors which, though they may be modified by external conditions, are nevertheless racial and transmissible.

Certain races are characteristically hard-grained, tending to produce strong flours. This is true of the wild wheats and of *T. monococcum* and *T. durum*. The degree of hardness may be modified but only within certain definite limits. On the other hand, the grains of *T. turgidum* are soft, and this is also true of many forms of *T. vulgare* and *T. compactum*. Here again the character may be modified.

In the bread wheats, marked variation is found. In particular, soil or climate or both may impress either characteristic upon the grain. Some of the strongest of the bread wheats are Austrian varieties. Tested in England, they were found to be weaker than the common English types. This is an extreme example of climate.

On the other hand, heavy soils tend to induce hardness, and also large dressings of nitrate of soda or sulphate of ammonia.

Certain bread wheats, however, are less plastic. Thus Red Fife—the parent of the American hard types—is as strong in England as in America. It is also of interest to note that Red Fife is not of American origin, but was first taken to Canada by a Scotsman called Fife in a sample of Danzig wheat!

MILLING OF WHEAT.—Three essential processes are found in milling:—breaking, reducing and separating.

1. Breaking process. The object of breaking is to tear open the grains with the minimum amount of friction. It is now carried out by means of rollers, one larger and also rotating faster than the other. These "breakrolls" split the

grain into particles of varying dimensions, the size depending on the distance between the two rollers.

2. Reducing process. Here the pairs of rollers are smooth, nearly equal in size and rotate at almost the same speed. They grind and reduce the particles.

3. Separating process. Separation is effected by shaking the products of the break and reduction processes on a fine sieve, and at the same time subjecting them to a current of air.

The sequence of events is as follows. After cleaning, the grain is passed through the first break. This produces some fine flour, a little fine husk and many moderate sized pieces of broken grain with adherent husk. The whole product is then separated into flour which falls through the sieve ; the husk which is mostly blown away ; and the larger particles.

These larger particles are then reduced between the smooth rollers, giving in the end much fine flour, more husk and still more smaller particles. The flour so obtained is termed " patents " and is the highest grade flour obtained.

The smaller particles are then sent through a second break, separated, again reduced and finally again separated. This gives more flour of a high grade, a considerable quantity of husk and still finer particles. A third and even a fourth break, each accompanied by separation, reduction and re-separation may follow. The fourth break scrapes the last traces of flour from the husk, but the flour as a consequence is less white because the rollers are now set so close that the husk is also powdered and tends to pass into the product.

In the process of breaking, the germs are not ground, but owing to their oily nature, flattened into small discs. These pass along the sieves without falling through owing to their size and shape. At the end of the sieve, they are collected.

We see then that modern milling gives us three products :—1, flours of various grades ; 2, husks, the so-called bran and sharps ; and 3, germs.

**PHOTOPERIODISM AND VERNALIZATION IN RELATION TO HABIT.**—Wheat and similar cereals, such as oats, barley and rye, are generally spoken of as long-day plants, flowering and fruiting in the summer days (or their equivalents) of temperate climates. They are, however, by no means equivalent in their reactions either to daylight or to temperature.

In the first instance wheat has been divided into two cultural classes—winter wheats and spring wheats. Winter wheats sown in autumn germinate at moderate temperatures, produce small, compact tillered plants which can survive low temperatures, and only commence to flower with increasing length of day the following season. Nevertheless their life period is annual. Sown in spring their behaviour is that of a biennial. During the first season they make vigorous vegetative growth and generally fail to ear ; flowering takes place in the subsequent season. Spring wheats on the other hand are always typical annuals. They germinate at moderate temperatures, make slow vegetative growth for a short period and thereafter ear rapidly with lengthening day. If sown in autumn the majority are killed by lack of hardiness to winter conditions.

The distinction is by no means absolute. Yet in the more advanced agricultural countries, the general reaction of most of the varieties is known with such accuracy that their behaviour in certain districts can be relied on.

Introductions from other districts or from other countries, however, may behave in a manner contrary to expectation. In other words the reactions appear to be fixed for certain areas, unpredictable for others.

Attempts have been made to differentiate winter and spring wheats on grounds other than physiological, but none of the criteria has proved decisive. Thus all winter forms are said to possess small dome-shaped growing points which do not elongate for a considerable period, whilst the growing points of spring wheats elongate very rapidly (15 to 20 days). Also, soft spring wheats are said to have longer and more pubescent leaves, accompanied by a relative lower chlorophyll content, than winter wheats.

As regards "winter hardiness," methods have been devised by which resistance to cold can now be estimated with considerable accuracy.

In a series of papers, Lysenko and his associates analysed the reaction of wheat and other cereals to temperature and daylight. In terms of their experiments, Lysenko advanced an explanation which differs markedly from that of earlier investigators.

The flowering of an annual plant is regarded by Lysenko as the last stage of a developmental sequence which is independent of the growth of the plant. Growth, as such, is quantitative: flowering is the result of a sequence of changes which follow in serial order, the changes being "qualitative," not quantitative in nature. The quantitative and qualitative stages may or may not coincide.

Each stage is conditioned by a definite set of external conditions such as temperature, light, moisture, aeration, etc., and must be completed before the succeeding stage can be initiated. If any one stage be omitted, the following stage is inhibited. Thus a winter cereal sown in spring lacks the essential conditions necessary for the initial developmental stage. As a consequence the plants remain for an indefinite period at the tillering stage, in spite of the fact that the conditions necessary for the subsequent stage are in operation. Interaction of the conditions may thus lead to the production of plants exhibiting (a) rapid growth and slow development; (b) slow growth and rapid development; (c) rapid growth and rapid development.

Two stages—perhaps three—pre-requisite for flowering have been recognized:

1. THE THERMO-STAGE.—The conditions here required are low temperatures, ranging from  $0^{\circ}$  to  $20^{\circ}$  C, according to the species or variety, and suitable conditions of moisture and aeration. Light and darkness play no part. This thermo-stage must be in operation and completed before the initials of the reproductive stage can be laid down. The time required for its completion does not depend on the size and age of the plant (*i.e.*, on its growth), but only upon its genotype and the environmental conditions. It can therefore be initiated not only in the growing plant but also in a seed which has just commenced development, but whose seed-coat is still unbroken. Upon this fact Lysenko has based his process of "vernalization."

For the completion of the first or thermo-stage, the different wheat varieties require different temperatures. In this respect they may be divided into three classes:—winter, semi-winter and spring forms. Winter forms require, together with other suitable conditions, temperatures not lower than  $-2^{\circ}$  and not higher than  $+10^{\circ}$ ; semi-winter forms, temperatures not lower than  $+3^{\circ}$  and not higher

than  $+15^{\circ}$ ; spring forms, temperatures from  $+5$  to  $+20^{\circ}\text{C}$ . Within each group, however, there is considerable variation, and the grouping is accordingly only approximate.

2. THE PHOTO-STAGE.—If the changes induced by the thermo-stage are complete, a further stage is necessary before reproduction can take place. This further stage is the "photo-stage." Here higher temperatures and either long-day conditions or short-day conditions for varying periods are essential.

In the case of wheat, the conditions are high temperature, plus long-day conditions, or better still, continuous illumination. Such plants could indeed be termed "plants of continuous illumination," for in the second stage they require continuous light for a definite period and only tolerate an alternation of day and night if the dark period be relatively short. "Short-day" plants, such as maize and millet (*Panicum*), behave quite differently. Following upon the thermo-period, they require a period of 10 to 15 days of continuous darkness in order to flower. Thereafter they can develop equally well in either a long or a short day. According to Lysenko, such "short-day" plants could be termed "plants which in one of their developmental stages require darkness or low light intensity."

3. THE THIRD STAGE.—According to Kraevõi and Kiričenko, a third stage, not yet fully elucidated, must follow the second. During this third stage, the changes essential to the formation of functional gametes are initiated. In wheat it appears to be dependent upon a length of day equivalent to at least 8 to 12 hours. Hence in the later stages, a shortening day is all that is required.

Summarizing the situation, the analysis indicates that a winter wheat is one which has the capacity to resist low temperatures, requires an initial developmental period of 40 to 50 days during which the temperature range varies from  $-2$  to  $10^{\circ}\text{C}$ , whilst light is of little or no importance; thereafter requires a period of higher temperature during which the ideal condition would be continuous daylight but in nature consists of what is termed "long-day"; and finally requires a light period equivalent to at least an 8-hour day for the formation of fertile gametes. On the other hand, a typical spring wheat has not the capacity to resist low temperatures. It requires for reproduction a sequence which is (1) a minimum period of 10 to 20 days, during which the temperature must range between  $5$  to  $20^{\circ}\text{C}$ , the light therein being unimportant; (2) a subsequent period at higher temperatures under continuous illumination or long-day conditions; and (3) a final period of illumination equivalent to at least an 8-hour day.

The distinctions, however, are not absolute. When a large number of varieties are studied, they form a graded series.

As already noted, Lysenko has based his process of "vernalization" ("Jarovizacija") on the fact that the "thermo-stage" can be induced in seeds which have just commenced their growth. Such seeds have—in so far as the embryo is concerned—ceased to be seeds in the physiological sense. Consequently, the first of the qualitative changes pre-requisite to development may then be induced in spite of the fact that practically no growth (quantitative change) has taken place.

In the case of "long-day" cereals, such as wheat, oat, barley and rye, the process is as follows. The seed must first be induced to germinate without the radicle breaking the seed-coat. This is done by adding water and keeping the

seed for 3 to 5 days at a temperature of 5 to 10° C. The amount of water to be added varies with the type ; for winter wheats, 37 litres per 100 km. of wheat ; for late spring wheats, 33 litres ; and for early spring wheats, 31 litres. Further, the water should be applied in three successive applications in order to ensure complete absorption, and thorough mixing is also essential.

When 3 to 5 per cent. of the seeds have burst their grain coats, vernalization commences, and the process is continued for 40 to 50 days in the case of winter wheats, 10 to 15 days for late spring wheats, and 5 to 6 days for early spring wheats. During these intervals, the seed must be maintained at the stage at which vernalization commenced. No further growth should be permitted, but the water content and a suitable temperature must be maintained throughout. If the grains become too dry, more water should be added ; if too moist, more grain. The most important factor, however, is the maintenance throughout the period of the correct temperature for the variety in question. These temperatures are 0° to 2 to 3° C for winter wheats, 3 to 5 to 6° C for late spring wheats, and 8 to 10° C for early spring wheats. The optimum temperature for any one variety within these classes—if not already known—must be determined by experiment.

During these respective periods, the embryos within the grain, being maintained at the correct temperature, undergo the whole of the qualitative changes of the thermo-stage of development. If sown immediately thereafter in spring, the subsequent developmental stages determined by light follow naturally, and the ears will form and ripen in advance of their normal period, the actual shortening of the period in each instance being theoretically equal to the time during which they were vernalized.

It is now claimed that the changes induced in the protoplasm by the main factors of each stage can be detected micro-chemically. Thus, if the thermo-stage be completed by vernalization, the growing points of such seeds stain an intense blue when treated with 5 per cent. ferric chloride followed by 5 per cent. potassium ferrocyanide. The growing points of untreated seeds or seeds that have only been partially vernalized remain unstained or become yellow or green. As the vernalization process passes towards completion, it is stated that blue-stained cells are found in increasing numbers scattered amongst the unstained cells.

By staining the epidermal cells with certain dyes, it is possible to detect the completion of the photo-stage. Thus the lower epidermis of wheat stained with a mixture of methylene blue and methyl red gave the following reactions : (a) pink—plants in which the thermo-stage was incomplete ; (b) blue—plants in which the thermo-stage was complete ; (c) mauve-pink—plants in which the photo-stage was complete.

These and similar experiments on the effects of light and temperature, however, have been variously interpreted. For example, Ljubimenko (1933) regards the changes produced as an " induction," which may, therefore, be retarded or accelerated and even reversed. Also, thermal and photoperiodic induction consist not in the specific preparation of the plant for reproduction, but in an acceleration of the entire developmental process. By maintaining the external factors at the requisite levels, both the reproductive and also the vegetative characters may be accelerated or retarded together. Vasiljev (1934) and Cailahjan (1934) consider that vernalization can be induced by light alone. Lebedinceva

studied the effect of chilling plus length of day and came to the conclusion that the usual distinction between long- and short-day plants is erroneous. Thus spring wheat and rye are true long-day plants; winter wheats on the other hand are only conditionally long-day plants, *i.e.*, they behave as long-day plants only after vernalization.

This viewpoint is similar to that advanced by Purvis (1934), who investigated the effect of day length on winter and spring rye after germination at 1° C and 18° C. In assigning the material to its photoperiodic category, she considered not merely the time of emergence of the inflorescence but in particular the time of formation of the flower primordia.

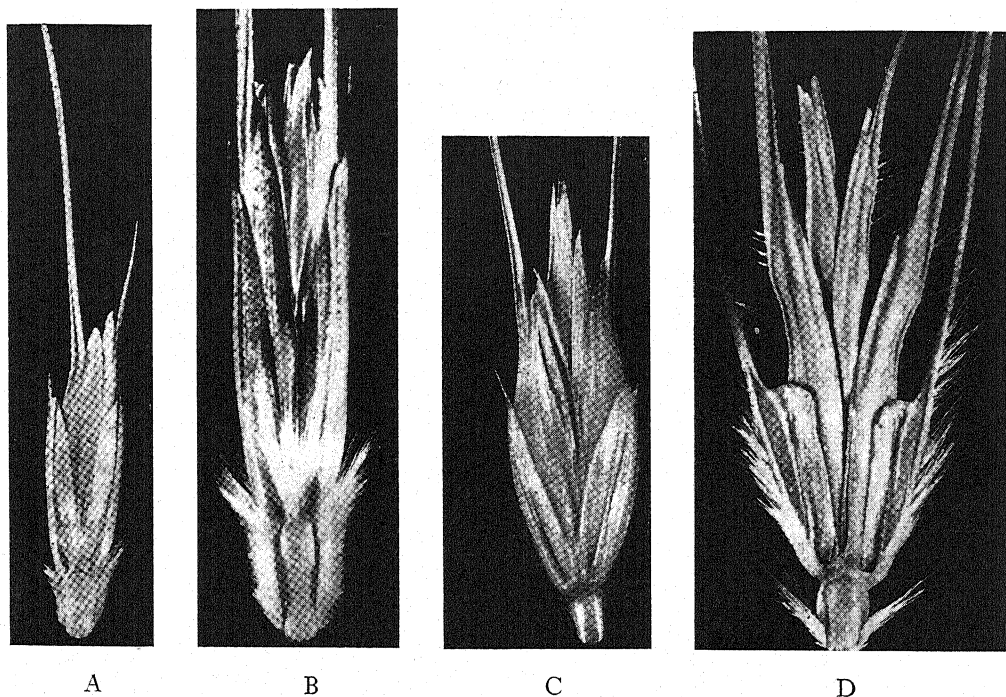


FIG. 48. Wild and adventive species of Wheat.

- A. *Triticum aegilopoides*, Bal.
  - B. *Triticum dicoccoides*, Körn.
  - C. *Triticum timopheevi*, Zhuk.
  - D. *Haynaldia (Triticum) villosa*.
- (After Sando.)

In winter rye, the differentiation of flower primordia was found to be subject to an interaction between day length and the temperature during germination, these factors determining both the minimal number of leaves formed before differentiation of flowers began, and the rate of growth of the meristematic tissue. As a consequence of this interaction, low temperature germination hastened flower inception in winter rye under long days, but produced no effect under short days. At the same time, after germination at high temperatures, short-day treatment led

to earlier differentiation of flower primordia than did long-day treatment. No temperature after-effect was found in spring rye, but short days retarded the differentiation of flower primordia. Once the differentiation of primordia had taken place, however, further development was always hastened by long days. Hence if ear emergence be taken as the criterion of flowering, all types of rye may be regarded as "long-day" plants; but if differentiation of flower primordia be taken into consideration, winter rye germinated at high temperatures. behaves as a short-day plant; germinated at low temperatures, it behaves as does spring rye.

**WHEAT SPECIES.**—Linnaeus in the first edition of his *Species Plantarum* (1753), classified the then known cultivated wheats under five species. Later, he added a sixth. Thereafter, the number of species recognized has varied from a minimum of three to a maximum of twenty. Percival (1921) enumerates two species and twelve "races" which might with equal justice be designated "cultivated species." Several additional species have since been described.

**I. THE GROUPS.**—Schulz (1913) showed that the species fall into three natural groups and subsequent writers have accepted and confirmed this conclusion. A fourth group has now been added.

TABLE XX.

## WHEAT SPECIES GROUPS.

Group I Einkorn	Group II Emmer	Group III	Group IV "Bread" or vulgare.
Chromosome No. 14 Genom System : AA.	Chromosome No. 28 Genom System : AABB	Chromosome No. 28 Genom system : AAGG.	Chromosome No. 42 Genom system : AABBDD
<i>Wild.</i> T. AEGILOPOIDES, Bal.	T. DICOCOIDES, Körn.	T. TIMOPHEEVI, Zhuck.	
<i>Cultivated.</i> T. MONOCOCCUM, L.	T. DICOCOCCUM, Schülb. T. DURUM, Desf. T. PERSICUM, Vav. T. ORIENTALE, Perc. T. PYRAMIDALE, Perc.  T. POLONICUM, L. T. TURGIDUM, L.		T. VULGARE, Host.  T. COMPACTUM, Host. T. SPAEROCOCCUM, Perc. T. SPELTA, L. T. MACHA, Dekaprevich et Menabde.

Sakamura (1918) working with root tips, found 14 chromosomes in *monococcum* (Group I); 28 chromosomes in *dicoccum*, *durum*, *turgidum* and *polonicum* (Group II); and 42 in *vulgare*, *compactum* and *spelta* (Group IV).



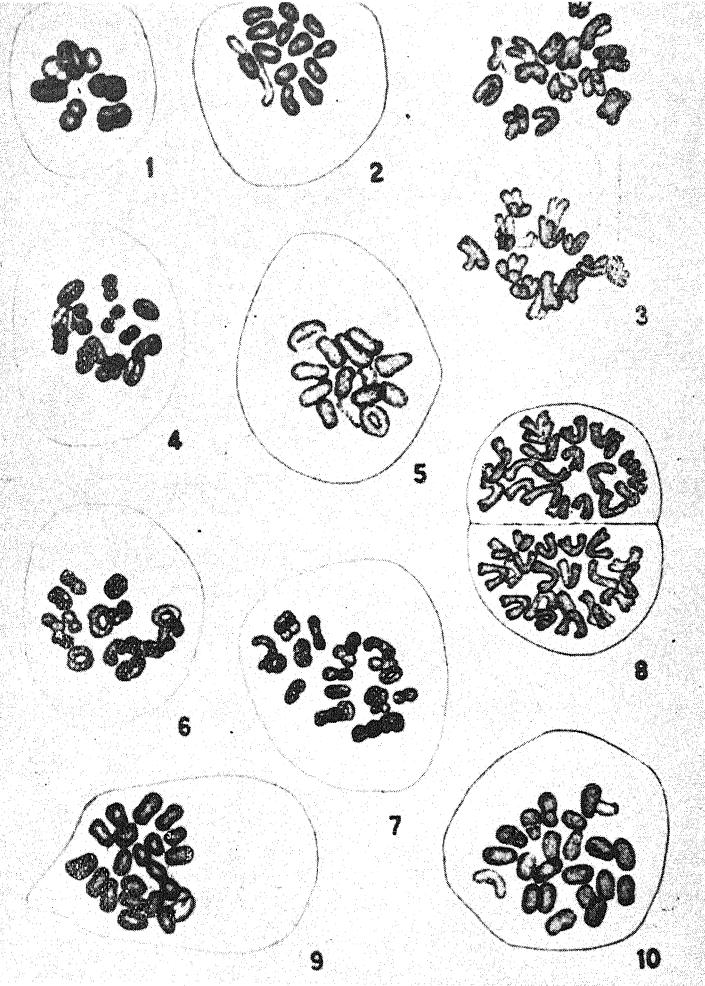


FIG. 49. Chromosomes of Wheat Species.

1. *Triticum monococcum* (Einkorn). Heterotypic equatorial plate, polar view; 7 paired chromosomes.
2. *Triticum dicoccoides* (wild wheat). Heterotypic equatorial plate, polar view; 14 paired chromosomes, one pair with chromosomes attached end to end.
3. *Triticum dicoccoides* (wild wheat). Heterotypic anaphase, side view; 14 chromosomes approaching each pole. Microspore mother-cell considerably flattened.
4. *Triticum dicoccum* var. Black Winter Emmer. Heterotypic equatorial plate, polar view; 14 paired chromosomes.
5. *Triticum turgidum* var. Alaska. Heterotypic equatorial plate, polar view; 14 paired chromosomes.
6. *Triticum durum* var. Kubanka. Heterotypic equatorial plate, polar view; 14 paired chromosomes. Many chromosomes tipped from the normal position.
7. *Triticum spelta* var. Bearded Spelt. Heterotypic equatorial plate, polar view; 21 paired chromosomes.
8. *Triticum spelta* var. Alstrom. Homoeotypic equatorial plates, polar view; 21 paired chromosomes in each cell of dyad.
9. *Triticum compactum* var. Hybrid 128. Heterotypic equatorial plate, polar view; 21 paired chromosomes.
10. *Triticum vulgare* var. Rudit. Heterotypic equatorial plate, polar view; 20 paired and 2 single chromosomes.

(After Aase and Powers.)

His figures were confirmed by Kihara (1919, 1921), who at the same time demonstrated the corresponding haploid numbers 7, 14 and 21, in the reduction divisions of the pollen mother-cells. These numbers have now been confirmed by many workers and for all the species of the four groups. It is therefore possible to settle to which group a doubtful form belongs by counting the chromosomes.

Additional criteria, however, are available. Thus, Tschermak (1914), Sax (1921), and subsequent writers have shown that the species within any one



FIG. 50.

Karyotypes of *Triticum aegilopoides* Bal (A) and *Triticum vulgare* v. *lutescens* Körn (B). (After Senjaninova-Korczagina.)

group are fully fertile *inter se*, but show varying degrees of sterility when intercrossed. The position in brief is as follows:

*Group I*  $\times$  *II* ( $7 \times 14$ ). Triploids. This cross is readily performed when the seed parent belongs to Group II (28), but not when it belongs to Group I (14). (Thompson, 1930.) The hybrids are nearly sterile, with approximately 98 per cent. of bad pollen. The number of bivalents is theoretically 7, but varies from 3 to 7 (average 5).

*Group I and III* ( $7 \times 14$ ). Triploids. The cross is fairly easy to perform and the hybrids are sterile. The number of bivalents varies from 4 to 7 (average 6), with multivalents not infrequent.

*Group I*  $\times$  *IV* ( $7 \times 21$ ). Tetraploids. The cross may be successful if the seed parent has the higher chromosome number (Bleier, 1928), otherwise it is difficult.

The hybrids are sterile or weakly fertile. There is little or no good pollen. The number of bivalents possible is generally less by 2 to 7.

*Group II*  $\times$  *III* ( $14 \times 14$ ). Tetraploids. With the wild species of II, the cross is easily performed and good pairing is secured. The hybrids are fertile. Crossed with cultivated forms (*T. dicoccum*, *T. persicum*, *T. pyramidale*, *T. durum*), the hybrids show bivalents varying from 7 to 14, with a tendency to a much looser association. There is, therefore, a lowering of the fertility which may approach to sterility.

*Group II*  $\times$  *IV* ( $14 \times 21$ ). Pentaploids. The crosses are more uniformly successful than those between the above groups.

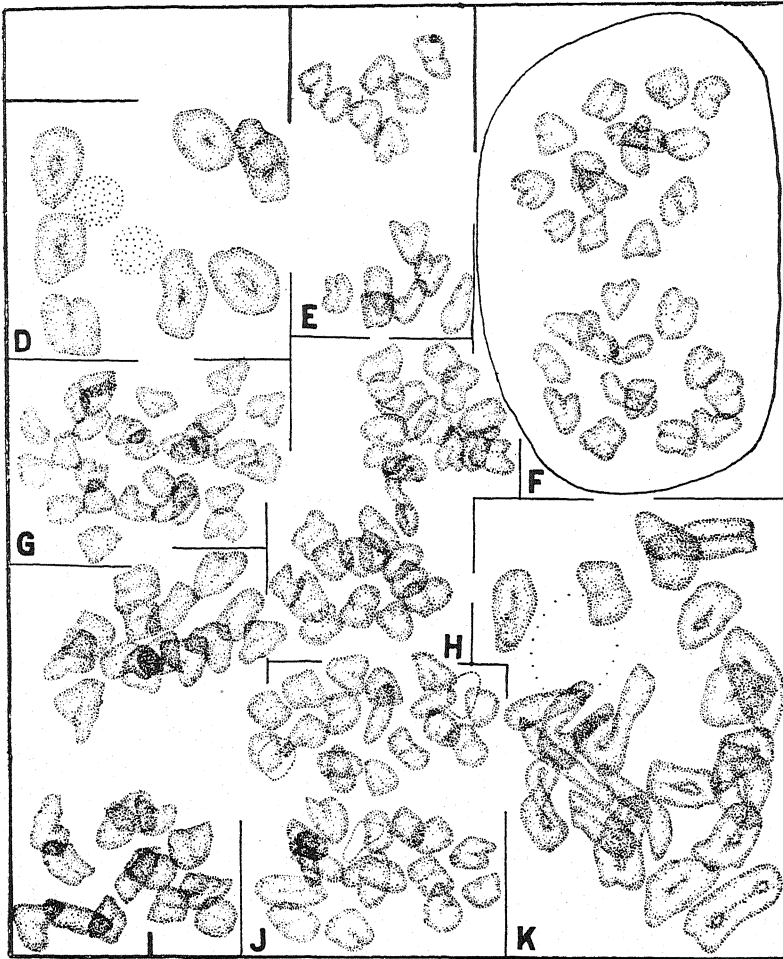


FIG. 51.

Chromosomes in *Triticum* species. X 2,000. D, diakinesis in *T. monococcum* L.; E, late heterotypic anaphase in *T. monococcum* L.; F, late heterotypic anaphase in *T. dicoccoides* Kcke.; G, heterotypic anaphase in a regular form of *T. polonicum* L.; H, heterotypic anaphase in *T. dicoccum* Schrk.; I, heterotypic anaphase in *T. turgidum* L.; J, heterotypic anaphase of an apparently fixed segregate of *T. vulgare*  $\times$  *T. polonicum*, showing 33 (-36?) chromosomes; K, diakinesis in *T. compactum* Host. (After Longley and Sando.)

The hybrids are moderately fertile, with some 15 per cent. of bad pollen. The chromosome number is 35, and at reduction there are 14 bivalents and 7 univalents.

*Group III*  $\times$  *IV* (14  $\times$  21). Pentaploids. The incompatibility is here surprising. When *T. Timopheevi* is used as the female parent with *T. vulgare* as the pollen parent, the grains set but shrivel and none germinates. No fertilization occurs in the reciprocal cross. An identical situation is found when *T. spelta* is employed.

Sax (1921) has shown further that the size of the pollen grains is different in three of the groups.

TABLE XXI.

DIAMETER OF POLLEN GRAINS IN WHEAT SPECIES.

Name.	Group.	Diameter of pollen grains in microns.	Average.
Einkorn	I	51.5	51.5
Kubanka (Durum)	II	55.5	56.3
Alaska (Turgidum)	II	57.1	56.3
Hybrid 143 (vulgare)	IV	60.1	60.2
Marquis (vulgare)	IV	60.3	60.2

Again, Vavilov (1914) found a similar grouping based on the susceptibility of the species to *Puccinia triticina*.

<i>Immune.</i>	<i>Resistant.</i>	<i>Susceptible.</i>
<i>T. monococcum.</i>	<i>T. durum.</i>	<i>T. vulgare</i> (a few immune).
	<i>T. polonicum.</i>	<i>T. compactum.</i>
	<i>T. turgidum.</i>	<i>T. spelta.</i>

The serological studies of Zade (1914) also lead to the conclusion that three natural groups exist. A similar method has been used by Nelson and Berkeland (1929) to differentiate varieties. The wheats showing the greatest number of factors in common possessed the closest serological relationships. On the other hand the results obtained by Edgecombe (1931) do not precisely parallel the cytological groupings. Thus the forms belonging to Group II appeared to be closely related serologically and to have marked affinities with those of Group I. But varieties of Group IV were less homogenous, some forms being more closely related to Group II than to the other members of their own group. It should be noted, however, that those forms of Group IV which showed serological affinities with Group II, were either immune or resistant to *P. triticina*, and that

one (the variety "Hope"), cytologically belonging to Group IV, is in origin a hybrid between an Emmer and a Vulgare.

Morphological differences between the members of the groups are difficult to define, a position accentuated by the wide range of variation, more especially among the members of the second and fourth group. Thus, Orlov (1922) has described 66 varying characters of *durum*, and Vavilov (1922) a similar number for *vulgare*. Watkins (1930) has made a comparative analysis of the two series of variables and points out that 55 of the characters analysed vary either in the same way in the two groups, or exhibit unimportant differences.

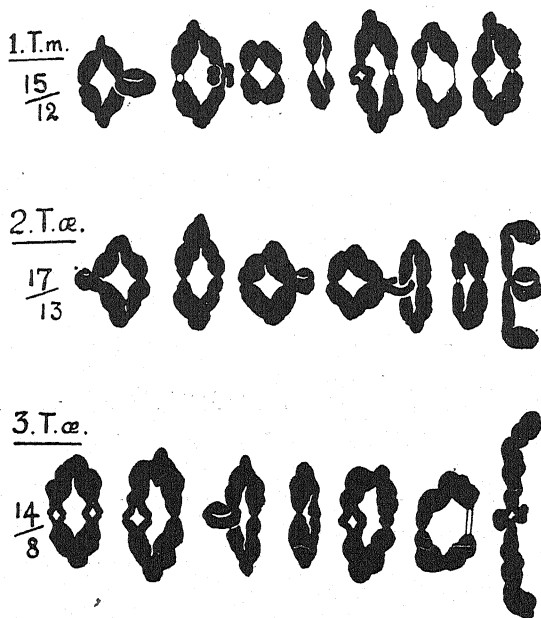


FIG. 52.

The bivalent chromosomes of *T. monococcum* (1) and *T. aegilopoides* ( $n=7$ ) (2 and 3). The total number of chiasmata and the number terminal is given at the side. Figs. 1 and 2, Flemming-gentian violet, X 3,200; Fig. 3, aceto-carmine, X 2,200. (After Darlington.)

### *Synopsis of Group Characteristics.*

Group I. Two species; chromosomes 14. Coleoptile 2-nerved; erect or prostrate; stem slender; ears bearded, compressed; spikelet 1- to 2-grained, terminal spikelet minute and abortive; rachis fragile, fracturing above the spikelet; glumes tough, long, narrow-keeled with stout apical tooth on the outer face; palea splitting longitudinally when ripe; grain small, finely pointed and compressed with indistinct furrow; tendency to rust immunity.

Group II. Six to seven species; chromosomes 28. Coleoptile usually 2-nerved, but 4 to 6 found; young shoots usually erect, sometimes prostrate, stems solid or hollow with thick walls; ears usually bearded;

terminate spikelet large and tending to become fertile ; rachis fragile (and then fracturing above the spikelet) to tough ; glumes usually long and narrow to short and blunt, generally keeled with variable apical tooth and with secondary tooth absent except in *dicoccoides* ; grains flinty to mealy, immune to resistant to rust.

Group III. One species only ; chromosomes 28. Coleoptile 2-nerved ; young shoots somewhat prostrate ; leaves with thick pubescence on the sheaths, but finer on the blades ; ears pubescent, somewhat brittle at maturity, very compact and broad ; glumes short, keeled ; lemmas longer than the glumes ; palea tending to split longitudinally at maturity, awns soft, thin and short. A weed species.

Group IV. Four to five species ; chromosomes 42. Coleoptile 2-nerved, erect to prostrate ; stems usually hollow (occasionally with solid upper inter-nodes) ; ears bearded or beardless ; rachis tough except in *spelta* when it fractures below the spikelet ; glumes keeled throughout or in upper half only ; apical tooth variable, short and blunt to short, acute or prolonged into an awn ; grain usually plump, mealy to flinty ; usually susceptible to resistant to rust.

## II. THE SPECIES.—A. *Species of Group I.*

### 1. *Triticum aegilopoides*, Bal. Wild Small Spelt.

Coleoptile : usually purple, 2-nerved.

Young shoots : erect, with broad leaves, or prostrate with narrow leaves ; leaves more or less finely hairy with longer hairs on the longitudinal ridges.

Stem : slender, erect, solid or hollow with thick walls, nodes with white deflexed hairs.

Ear : bearded and compressed ; narrow across the face, broad across the 2-rowed profile.

Rachis : fragile, disarticulating from above downwards, smooth ; fringed along the margins and with tuft of whitish hairs at each node in front of the spikelet.

Spikelet : terminal spikelet abortive ; others 2-flowered, the lower fertile, the upper usually sterile.

Glumes : tough, long, narrow, keeled throughout with stout acute tooth often pointing outwards ; prominent lateral nerve ending in secondary tooth.

Lemmas : scabridly awned, the awn of the upper flowers tending to reduction ; palea entire, splitting longitudinally at maturity.

Grain : small, pointed at both ends, compressed ; furrow indistinct, flinty ; apical brush scanty to large ; olive-yellow, pink, red to greenish in colour.

*T. aegilopoides* is widely distributed in parts of the Balkans, Asia Minor, the Crimea, Transcaucasia, Palestine and Syria to the borders of Persia. Percival describes four varieties. Flaksberger and others make two species—*T. aegilopoides*, Bal., with 1-awned spikelets and *T. Thaouder* with 2-awned

spikelets. In each species about five varieties have been described and the precise distribution of these forms is now better known. (Flaksberger, 1926 ; Jacobziner, 1932, a and b ; Dekaprelevisch and Menabde, 1932 ; Troitzky, 1932.) The Mediterranean forms are said by Vavilov to be larger than the Asiatic forms. There is also marked parallelism between the wild Einkorns and the wild Emmers.

2. *Triticum monococcum*, L. Einkorn or Small Spelt.

Coleoptile : 2-nerved.

Young shoots : prostrate, semi-erect to erect ; leaves narrow ; hairs few and very short.

Stem : slender, erect, usually hollow with thin walls ; nodes with deflexed hairs.

Ear : bearded and compressed, much narrower across the face than the 2-rowed profile ; denser than *aegilopoides*.

Rachis : flattened, fragile, glabrous or at times fringed, with tufts of hair as in *aegilopoides*.

Spikelet : terminal minute, infertile ; others 3-flowered, but 1- or 2-grained only.

Glumes : tough, long, narrow, keeled throughout with stout, acute tooth, straight or turning inwards ; prominent lateral nerve ending in secondary tooth.

Lemmas : longer than the glumes with terminal sinus and straight scabrid awn ; awn short or absent on upper florets.

Paleae : entire, but splitting at maturity.

Grain : as in *aegilopoides* but shorter.

Small Spelt has been cultivated since pre-historic times in Western Europe and parts of Asia Minor, but is now of very minor economic importance. Körnicke has described three varieties.

B. *Species of Group II.*

3. *Triticum dicoccoides*, Körn. Wild Emmer.

Coleoptile : usually purple, 4-nerved.

Young shoots : prostrate ; leaves narrow with short relatively coarse hairs or, according to Percival, fine soft hair.

Stem : slender, solid or (according to Percival) hollow with thick walls ; nodes with deflexed hairs.

Ears : bearded, compressed, much narrower across the face than the 2-rowed profile ; somewhat lax.

Rachis : fragile, disarticulating above the spikelet, flattened, smooth, shining with conspicuous lateral fringe of long white, yellow or dark-brown hairs.

Spikelets : terminal, usually sterile ; others 3-flowered but 1- (or 2-) grained.

Glumes : tough, long, narrow, glabrous or with silky hairs, with strong scabrid keel with blunt or acute tooth, straight or curving inwards or outwards ; prominent nerve ending in secondary tooth.

Lemmas : somewhat shorter than glumes, slightly divided at apex with strong scabrid, slightly dorsal awns.

Palea : divided at tip, not splitting at maturity.

Grain : very long, narrow, pointed at both ends, triangular in outline, apical brush of long, whitish hairs.

*T. dicoccoides* was first noted by Körnicke in 1873, as a portion of an ear mounted with a herbarium specimen of *Hordeum spontaneum*. Aaronsohn rediscovered the plant at Rosh Pinar in 1906. It appears to be widely distributed in Palestine, Syria, Armenia, Transcaucasia and Western Persia, and the evidence that it is a truly wild species is now convincing.

Percival (l.c) described five varieties. A much larger number is now known. Jacobziner (1932) has described many of these forms, and has tabulated the essential differences between the Armenian types and the types of Palestine and Syria.

It is of interest to note that Love and Craig (1919) produced a synthetic type morphologically similar to *T. dicoccoides* from a cross between *T. vulgare* (Early Red Chief) and a *T. durum* (Marouani). Further tests (1924) indicate that the synthetic form behaves genetically as does the wild.

#### 4. *Triticum dicoccum*, Schülb. Cultivated Emmer.

Coleoptile : 4- to 6-nerved in Indo-Abyssinian types ; 2-nerved in European types.

Young shoots : usually erect, with short hairs of nearly uniform length on the young leaves ; auricles pinkish, fringed in European forms, more or less glabrous in Indo-Abyssinian forms.

Stem : somewhat slender, solid or hollow with thick walls.

Ear : bearded, compressed, narrower across the face than the profile.

Rachis : fragile or tough, disarticulating above the spikelets, rarely tending to cohere ; flattened, smooth, more or less hairy along the margins, each segment narrow below and widening considerably above.

Spikelets : all more or less fertile, 3- to 4-flowered, setting typically 2 grains.

Glumes : Long, narrow, strongly keeled with apical tooth acute and curved or short and blunt ; outer face flat.

Lemmas : with 3-angled awns.

Palea : ovate-lanceolate with narrow bifid apex.

Grains : long, narrow, pointed at both ends, ventral side flat to slightly concave and with narrow furrow ; flinty to semi-flinty.

The species as described by Percival is a complex one, including (1) *T. dicoccum*, Schrk. (2) Indo-Abyssinian forms with a tough rachis, and (3) *T. persicum*, Vav. He divides the species as follows :—

Group I. Indo-Abyssinian with 4-nerved coleoptiles.

Section A : Speltae. Rachis fragile.

Section B : Tenaces. Rachis tough.

Group II. European Emmers with 2-nerved coleoptile.



In this grouping, *T. Persicum* of Vavilov falls into Section B of Group I.

Emmer wheat is now restricted in cultivation to the more backward and primitive districts. Formerly, it had a much wider distribution. There is for example evidence of its cultivation in Neolithic times in Switzerland (Heer), and in Denmark, Germany and Bohemia (Schültz, 1916). That it was widely cultivated in Ancient Egypt is now accepted (see Percival, 1921), and according to Hazny, it was the chief cereal cultivated in Babylonia. Its gradual replacement by Durum and Vulgare wheats took place in the Graeco-Roman period. (See also Stoletova, 1924; Flaksberger, 1928.)

5. *Triticum orientale*, Perc. Khorasan Wheat.

Coleoptile : 2-nerved.

Young shoots : erect, with very narrow pubescent leaves.

Stem : thin, of medium height, solid or hollow with thick walls.

Ear : bearded, very lax and almost square.

Rachis : tough with fringed margins ; inter-nodes narrow and wedge-shaped.

Spikelets : all fertile, 3-flowered, 2- to 3-grained.

Glumes : long, narrow, keeled to the base, with blunt apical tooth, lateral nerve prominent ; white and pubescent.

Lemmas : with scabrid, usually deciduous awns.

Grain : very long, narrow and flinty.

Percival reports the species as a small distinct race cultivated on irrigated land in Persia. It is regarded as a form of *durum* by Jacobziner (1932).

6. *Triticum durum*, Desf. Durum or Macaroni Wheat.

Coleoptile : 2-nerved.

Young shoots : erect ; quite glabrous or nearly so.

Stem : tall, solid or hollow with thick walls.

Ear : bearded, square or narrower across the face than the profile.

Rachis : usually tough or disarticulating somewhat, especially towards the base ; margins fringed with frontal tuft of hairs at the spikelets.

Spikelets : somewhat long and narrow, 5- to 7-flowered, 2- to 4-grained.

Glumes : long and narrow, outer face somewhat flattened, glabrous or hairy, with prominent, curved keel from base to tip, and strong inwardly curved apical tooth.

Lemmas : 9- to 15-nerved, thin, pale and rounded on the back ; the awns long, almost smooth at the base diverging slightly ; those of the upper lemmas of a spikelet usually shorter.

Grain : long, narrow, flinty, more or less pointed at both ends ; dorsal ridge prominent ; crease shallow with sloping sides ; cross-section somewhat triangular.

The Durums are the only group of 28 chromosome wheats which have survived in extensive cultivation into the present period. From an economic standpoint, owing to their drought resistance, coupled with their resistance to rust and other fungi and the inherent " strength " of the grain, the Durum wheats

are, especially in the warmer and somewhat arid districts, of equal importance to the Vulgare wheats. Their characters have recently been studied in great detail by the Russian investigators.

7. **Triticum Polonicum**, L. Polish Wheat.

Coleoptile : 2-nerved.

Young shoots : erect ; young leaves blue-green and glabrous.

Stem : tall, solid or hollow with thick walls.

Ear : bearded, somewhat square, lax to medium.

Rachis : somewhat fragile ; flattened and smooth ; margins fringed ; frontal tuft of hair to each spikelet.

Spikelets : bearded ; large and flattened ; 4- to 5-flowered, 1- to 2- (or 3-) grained.

Glumes : as long as, or longer than the spikelet ; lanceolate and narrow, keeled throughout, the keel fringed and ending in a short tooth ; secondary tooth small or absent.

Lemmas : boat-shaped, rounded on the back ; 15- to 17-nerved, edges fringed with short hairs ; the two lowest lemmas distinctly awned, the upper shortly awned or not awned.

Grain : very long, narrow, yellowish-white or pale red ; flinty ; somewhat triangular.

Polish wheat appears to be of comparatively recent origin, but as it possesses no characteristics which are not found in a higher degree in the Durums, its cultivation has always been limited.

8. **Triticum turgidum**, L. Rivet or Cone Wheat.

Coleoptile : 2-nerved.

Young shoots : erect or prostrate ; with short narrow leaves, usually dark-bluish-green, covered with soft hair of nearly uniform length.

Stem : tall, solid or hollow with thick walls.

Ear : usually bearded ; square, or narrower across the face than the 2-rowed profile ; often pendulous.

Rachis : tough ; margins densely fringed with white hairs, similar frontal tuft before each spikelet.

Spikelets : about as long as broad ; 5- to 7-flowered ; 3- to 5-grained.

Glumes : tough, short and broad ; the outer face convex, 5- to 7-nerved, prominently keeled throughout, the keel ending in a stout, usually acute and curved tooth ; prominent lateral nerve often present.

Glumes : sometimes ending in a short secondary tooth.

Lemma : thin and fragile ; oval and boat-shaped with 9 to 15 fine nerves, awns stout, triangular in section, scabrid and sometimes deciduous.

Grain : large, plump and somewhat short ; mealy ; apex truncate ; dorsal crest behind embryo high ; furrow shallow, with rounded cheeks.

The Rivet wheats are high yielding but the flour is "weak." They are intensively cultivated in certain localities, but are not widely distributed.

9. *Triticum pyramidale*, Perc. Egyptian Cone Wheat.

Coleoptile : 2-nerved.

Young shoots : erect ; with soft hairs of nearly uniform length on the leaves (this velvety pubescence is said by Jacobziner (1932) not to be typical) ; older leaves yellowish-green.

Stem : short, solid or hollow with thick walls.

Ear : bearded, short, dense, tending to taper towards the apex narrower across the face than the 2-rowed profile.

Rachis : tough ; margin fringed with white hairs ; frontal tuft before each spikelet.

Spikelets : more or less square ; 3- to 4-grained.

Glumes : tough, strongly keeled throughout, apical tooth long and acute, or short and blunt.

Lemmas : with slender awn, scabrid to the base.

Grain : usually white ; short, narrow, somewhat pointed at apex ; dorsal hump prominent.

Egyptian Cone wheat is a small group, first described by Percival from Egypt. Jacobziner (1932) considers that it is really a durum.

C. *Species of Group III.*10. *T. Timopheevi*, Zhuk.

Coleoptile : 2-nerved.

Young shoots : more or less prostrate ; leaf sheaths with long white dense hairs, similar but less dense hairs on the leaves.

Ear : bearded, compact and broad ; wider across the face than the profile.

Rachis : somewhat brittle at maturity ; pubescent, with thin short hair.

Glumes : somewhat short ; keeled ; no wing-like appendages.

Lemmas : thin, membranous and awned ; awns soft, thin and short.

Palea : tending to split longitudinally at maturity.

Grain : small and somewhat pointed.

A wild species found in high mountainous regions in Georgia. It is markedly resistant to rust, smut and mildew.

D. *Species of Group IV.*11. *Triticum vulgare*, Host. Bread Wheat.

Coleoptile : 2-nerved.

Young shoots : erect, semi-erect to prostrate ; young leaves with long hairs on the summit of the longitudinal ridges with shorter hairs often present on the flanks.

Stem : variable in height ; hollow with thin walls, occasionally with solid upper inter-nodes.

Ear : bearded to beardless ; variable in density ; square or broader across the face than the 2-rowed profile.

Rachis : tough, fringed with short hairs on the margins ; a few hairs at the base of each spikelet.

Spikelets : about as long as broad ; 5- to 9-flowered ; ripening 4 to 5 grains towards the centre, usually fewer at base and apex.

Glumes : loose, broad, the outer face convex ; usually keeled in upper half only and then with rounded base ; rarely keeled throughout ; apical tooth in bearded forms short and acute, or prolonged into an awn (1 to 4 cm. long) ; in beardless forms usually short and blunter.

Lemmas : thin, pale, rounded on back with 7 to 11 nerves ; awns when present, scabrid, triquetrous and persistent, sometimes short, stout and brittle ; usually straight or slightly curved, very rarely twisted or bent.

Grain : varied, usually plump with bluntish apex ; crease shallow, cheeks convex and plump ; dorsal side rounded without hump or ridge ; flinty to mealy.

The Bread Wheats are very variable, and include a vast assemblage of varieties, which may be due to a hybrid origin. Various classifications of the varieties have been attempted.

12. ***Triticum compactum***, Host.

Coleoptile : 2-nerved, pinkish or colourless.

Young shoots : usually erect, at times semi-erect to prostrate ; with yellowish-green or blue-green leaves, usually with hairs as in *vulgare*.

Stem : erect, stiff, generally hollow with thin walls, very rarely solid.

Ear : bearded or beardless ; short and dense ; oval or oblong, at times "clubbed," square in section.

Rachis : tough ; fringed with hairs along the margins and across upper part of each notch below the spikelet.

Spikelets : broad and short ; 6- to 7-flowered, 3- to 5-grained.

Glumes : as in *T. vulgare*.

Lemmas : inflated, with scabrid, sometimes widely diverging awns in bearded types.

Grain : small, oval and narrow towards the apex and plump ; crease shallow, with plump cheeks ; dorsal side sometimes with prominent hump ; mealy to occasionally flinty.

This ancient species is widely cultivated but only to a limited extent.

13. ***Triticum sphaerococcum***, Perc. Indian Dwarf Wheat.

Coleoptile : 2-nerved.

Young shoots : erect ; with leaves as in *T. vulgare*.

Stem : very short, stiff, erect and hollow.

Ear : bearded or beardless, less dense than *T. compactum*, stiff and erect.

Rachis : tough ; margins fringed with white hairs extending along the front below each spikelet.

Spikelets : more or less square ; 6- to 7-flowered ; 4- to 5-grained.

Lemmas : broad and short, inflated, usually keeled above ; apical tooth strong, curved and scabrid.

Grain : very short, somewhat truncate to angular ; flinty.

This wheat, first separated from *T. compactum* by Percival, is grown in the Central and United Provinces in the Punjab, India. It is also known in Persia.

14. **Triticum spelta**, L. Large Spelt.

Coleoptile : 2-nerved.

Young shoots : erect or prostrate ; with dark green leaves, slightly hairy as in *T. vulgare*.

Stem : stout and hollow with thin walls.

Ear : bearded or beardless ; relatively long and lax, more or less square.

Rachis : fragile, disarticulating below the spikelets ; broad and stout ; convex on one side, flat or concave on the other ; margins more or less hairy with very small or no frontal tuft of hairs.

Spikelets : narrow and oval, convex in section ; 3- to 4-flowered ; 2- to 3-grained, except the upper spikelets which usually ripen one grain.

Glumes : loose, with broad truncate apex and parallel nerves ; keel prominent throughout, ending in short, blunt apical tooth ; strong lateral nerve ending in blunt projection some distance from the apical tooth.

Lemmas : boat-shaped, thin, 9- to 11-nerved ; awn, a short claw-like projection or a true stiff scabrid awn.

Grain : long, somewhat pointed at both ends ; ventral surface flattened or hollow ; shallow crease ; section slightly angular, usually flinty.

Spelt wheat is generally believed to be of comparatively recent origin. In Europe, it is found mainly in two centres—S. Western Germany where it is confined to the mountain systems of the N. Western Alps, the Vosges, the Black Forest and the Swabian Alps ; and the Austrian province of Spain where it occurs in the Cantabrian mountains. Its cultivation elsewhere is very scattered and up to recently neither true Spelt nor any allied form was known in the East. Flaksberger accordingly suggested that Spelt was derived locally from *T. vulgare* at a comparatively recent epoch. On the other hand, Percival (1921) believed that it was a segregate from a hybrid of a wheat of the Emmer group with *Aegilops cylindrica*. Either supposition might be correct. The discovery, however, of closely allied Spelt forms in Asia (Dekaprevich and Menabde, 1932) alters the situation, and tends to support Vavilov's theory that all 42-chromosome wheats are of Asiatic origin.

15. **Triticum Macha**. Dekapr. et Menabde. "Makha" wheat.

Coleoptile : (? 2-nerved).

Young shoots : prostrate to spreading ; narrow-leaved, purplish to green ; older leaves also narrow but dark green ; glabrous (small spines) or with very sparse hairs ; auricles green or purple.

Stems : About 100 cm. long ; hollow throughout ; nodes slightly to strongly pubescent.

Ears : Semi-bearded ; long and lax to comparatively dense.

Rachis : fragile, generally disarticulating above the spikelets as in *T. dicoccum* ; broad and distinctly convex on one side, concave on the other.

Spikelets : 3- to 4-flowered, ripening usually 2 grains ; short to long and broad : often densely pubescent at the base and sometimes above, especially on the ribs.

Glumes : varying from " spathulate " with broad shoulder to lanceolate with no shoulder ; several nerved and usually prominent, with one lateral nerve marked and nearly always ending in a second tooth ; apical tooth obtuse or acute, slightly curved, incurved or hooked.

Grain : semi-flinty and red in colour ; ventral side flat or with depression ; crease broad and deep ; dorsal side often wrinkled, with longitudinal furrows due to pressure of the nerves of the glume.

This species, recently described by Dekapreleitch and Menabde (1932), is common in W. Georgia. According to these authors, it is fairly close to but nevertheless distinct from *T. Spelta*. The presence of such wheats in Georgia, many of them " intermediate " between *T. Spelta* and *T. vulgare*, they regard as further proof of the origin of all 42-chromosome types in S.W. Asia. They incline to the opinion that *T. Macha* is the main primary group and that *T. Spelta* is a secondary monomorphous group derived from *T. Macha*, probably at a comparatively recent epoch.

III. THE VARIETIES.—In many of the above papers and monographs, the cultivated varieties of the species have been described. Their identification, however, is by no means simple, and is complicated by difficulties in the nomenclature. At present, all such classifications should be regarded as " classificatory guides." (See, for example, Boutineau, 1900 ; Howard, 1909 and 1910 ; Stoll, 1920 ; Percival, 1921 ; Orlov, 1922 ; Vavilov, 1922 ; Archer, 1923 ; Clark et al., 1923 and 1935 ; Stewart, 1925 ; Zhukovski, 1925, etc.)

CYTO-GENETICAL STUDIES.—Inter-varietal crosses and interspecific crosses between the species of the same group and between the species of the different groups have been extensively conducted. Certain intergeneric crosses have also been studied, though in less detail. Thus the discovery by Requier in 1821 of a wheat-like plant, which he termed *Aegilops triticoides*, produced a fierce controversy as to the origin of wheat, and stimulated interest in the inter-relationships of *Triticum* and *Aegilops*. As a consequence, hybridization of *A. ovata* with wheat pollen was attempted and successfully secured by Godron in 1854. Later, interest in *Aegilops*-*Triticum* waned, but has recently been revived by Percival's hypothesis that *T. vulgare* and the other 42-chromosome wheats are the result of inter-crossing between *T. dicoccoides* and *Aegilops cylindrica* and *A. ovata*. The evidence that wheat-barley crosses have been obtained is inconclusive ; on the other hand, wheat-rye crosses have been secured without much difficulty. Recently, intergeneric crosses between wheat and *Agropyron* spp. have aroused interest.

Mutations—if the speltoid forms are excepted—are comparatively rare in wheat. The mutation rate has been studied by Stadler (1929). Induced mutations

through the use of X-rays, etc., have also been obtained. The most extensive studies have been those of Muller and Delaunay (1930, 1931, 1932). With Rontgen-rays, Delaunay found that considerable sterility was produced, but both factor mutation and chromosome aberrations resulted. With X-rays there

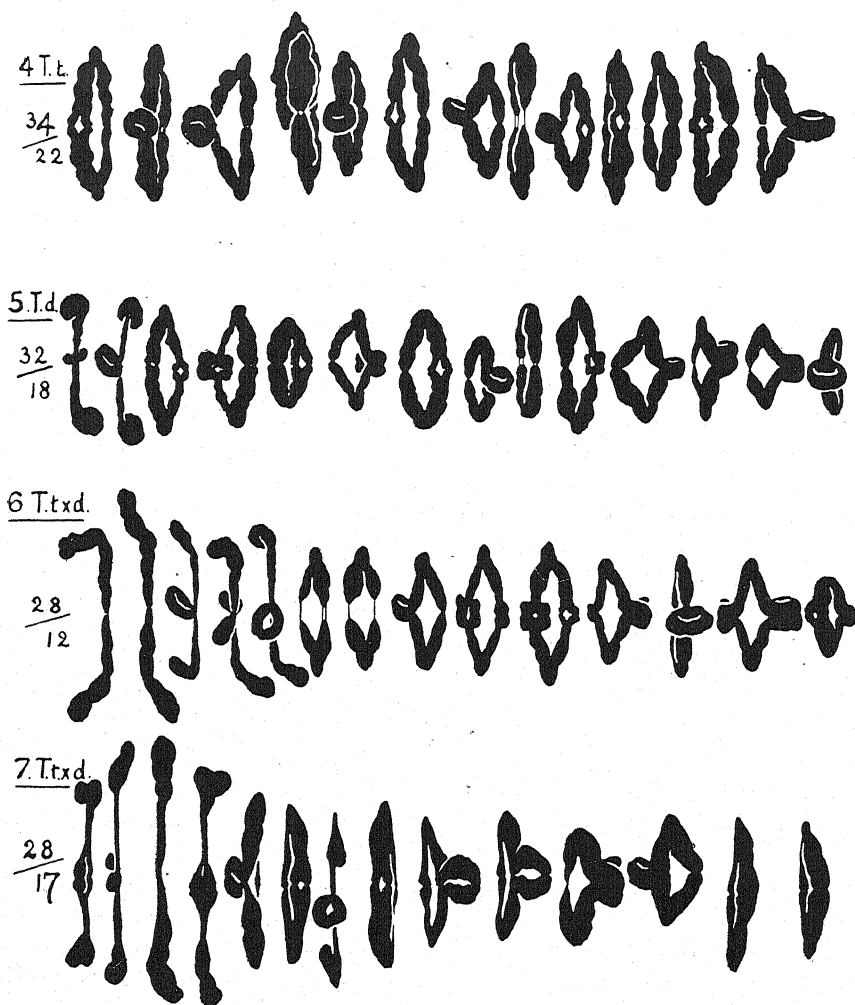


FIG. 53.

The bivalent chromosomes of *T. turgidum* (4), *T. dicoccum* (5) and their F<sub>1</sub> hybrid (6 and 7) ( $n=14$ ). 4,  $\times 2,200$ ; 5-7,  $\times 3,200$ . The total number of chiasmata and the number terminal are given at the side of each. (After Darlington.)

was also considerable sterility, but ears irradiated during the reduction division gave rise to eight undoubted mutants. At least one mutant, and probably a second, was a locus mutation; the remainder were chromosome aberrations.

I. INTER-SPECIFIC CROSSES BETWEEN MEMBERS OF THE SAME GROUP.—As noted above, crosses between species of the same group are

readily performed, and the hybrids are completely fertile. In the  $F_2$  generation, simple Mendelian segregation of contrasting characters is met with, but duplicate and triplicate factors for certain characters are also well known. Failure to segregate was found by Biffen (1916) in a cross between a white chaffed *polonicum* and a grey-chaffed *turgidum*. Again, although the cross long-glumed *polonicum*  $\times$  short-glumed *durum* gave a 1 : 2 : 1 segregation in the  $F_2$ , the extracted pure long forms were far shorter than the original parents (Caporn, 1918). This phenomenon, termed "shift" by Engledow (1920, 1923), has been noted in other instances. Its occurrence has been explained on the basis of autosyndesis by Darlington (1927), and on the basis of linked chromosomes by Malinowski (1926).

In the course of certain of these hybrid investigations, a number of aberrant forms have been obtained. The most frequent have been the speltoids and derivatives therefrom discussed below. Dusseau (1932, 1933, 1934) obtained, in the  $F_2$  of a cross between two varieties of Vulgare, a wheat of the Durum type. Subsequent study of the segregate showed that it was a constant type, with 14 somatic and 7 haploid chromosomes. It must, therefore, be regarded as a haplodurum, which Dusseau considers may have arisen from the loss of the A and C genomes of the original parents. Further durum and durreloid forms have since been obtained with  $2n = 28$  chromosomes (Miège and Simonet, 1933; Dusseau, 1934).

II. INTER-SPECIFIC CROSSES BETWEEN MEMBERS OF DIFFERENT GROUPS.—A. *Diploid* ( $n = 7$ ) by *Tetraploid* ( $n = 21$ ) *Species*.—As already mentioned the cross is readily performed when the seed parent belongs to the second group, but not when it belongs to Group I ( $n = 7$ ). Such hybrids have been studied by Sax (1922) in *T. monococcum*  $\times$  *T. turgidum*; by Kihara (1924) in *T. dicoccum*  $\times$  *T. monococcum* and *T. aegilopoides*  $\times$  *T. dicoccum*; by Thompson (1926) in *T. monococcum*  $\times$  *T. turgidum*; by Bleier (1930) in *T. dicoccoides*  $\times$  *T. aegilopoides*; by Aase (1930) in *T. durum*  $\times$  *T. monococcum*, and *T. dicoccoides*  $\times$  *T. monococcum*; by Thompson (1930) in *T. monococcum*  $\times$  *T. durum* and *T. turgidum*; by Longley and Sando (1930) in *T. dicoccoides*  $\times$  *T. monococcum*, *T. turgidum*  $\times$  *T. monococcum* and *T. polonicum*  $\times$  *T. monococcum* and by others.

The hybrids are triploid with 21 chromosomes. They exhibit resemblances to both parents, but those of the 28 chromosome-parent predominate. Out of 13 pairs of characters, Thompson found seven of the durum characters partially or completely dominant and three of the monococcum partially dominant. The hybrids are markedly infertile, approximately 98 per cent. of the pollen being shrunken and empty. Thompson failed to obtain seed by back-crossing with the monococcum parent; with the 28 chromosome-parent, a few seeds were obtained. When the plants are grown unprotected, he estimated that about 1 flower in 800 or 900 set grain. In protected spikes the number of grains set showed further reduction.

In the reduction division of the  $F_1$  hybrids, 7 bivalents and 7 univalents may form. Presumably the 7 bivalents consist of the 7 Einkorn chromosomes which have paired with 7 of the Emmer. The number of bivalents, however, shows marked variation. Sax (1922) found they ranged from 5 to 7; Kihara (1924), 4 to 7; Thompson (1926), 3 to 7; Kihara and Nishiyama (1928), 4 to 7



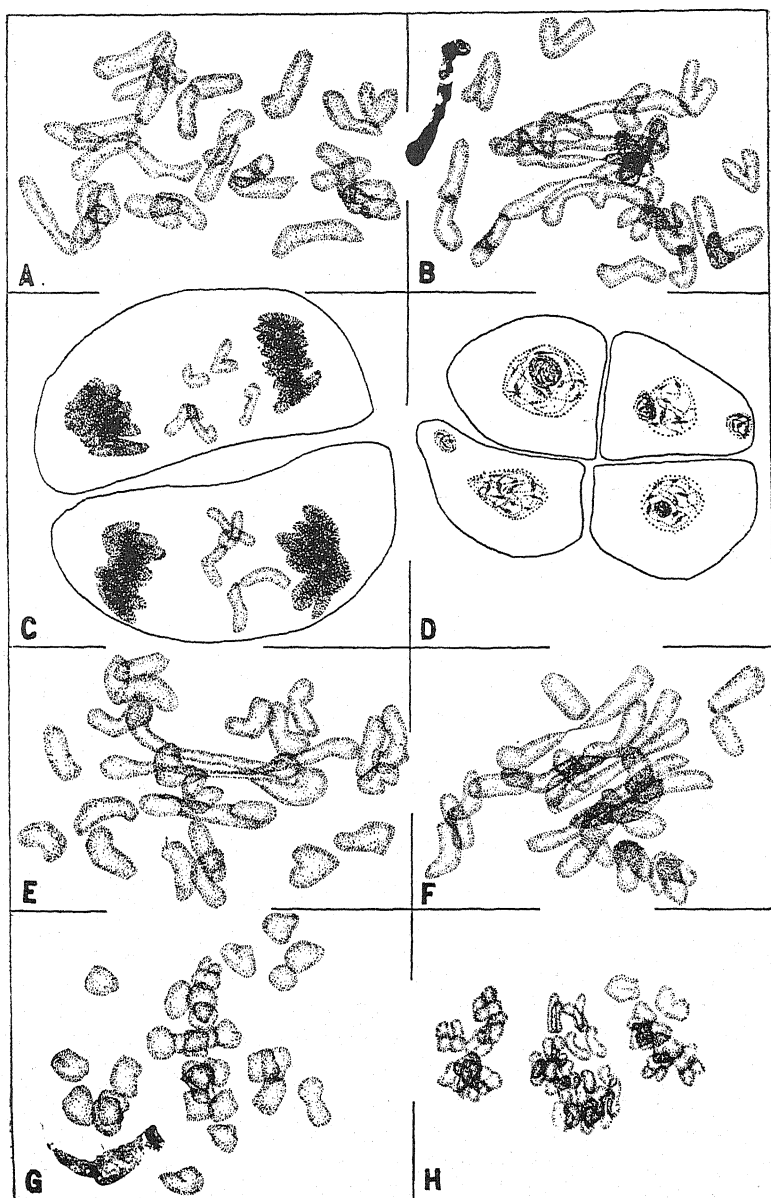


FIG. 54.

Chromosomes in *Triticum*  $\times$  *Triticum* hybrids.  $\times 2,000$ : A, Heterotypic prophase in *T. spelta*  $\times$  *T. monococcum*; B, heterotypic metaphase in *T. spelta*  $\times$  *T. monococcum*; C, homotypic anaphase in *T. spelta*  $\times$  *T. monococcum*; D, tetrad in *T. spelta*  $\times$  *T. monococcum*; E, F, G, three heterotypic metaphases in *T. vulgare*  $\times$  *T. monococcum*; H, heterotypic anaphase in *T. vulgare*  $\times$  *T. monococcum*. (After Longley and Sando.)

with from 0 to 3 trivalents; Bleier (1930), 0 to 5; Aase (1930, a and b), 4 to 7; Longley and Sando (1930), 0 to 6, 0 to 7 and 0 to 5.

In the F<sub>2</sub> generation, unexpected chromosome numbers were obtained by Thompson (1931). There were no segregates approaching the chromosome numbers of *monococcum* ( $2n = 14$ ). The majority had 28 or more chromosomes; a few had 35 and 42. Apparently, F<sub>1</sub> gametes with fewer than 14 chromosomes did not function. The functional gametes had approximately 14 or 21 chromosomes.

The hexaploid wheat plants obtained had not the characters of common hexaploids (*i.e.*, of the *vulgare* group).

On the other hand, although no segregates with chromosome numbers approximating to those of *monococcum* were obtained, each *monococcum* character appeared in a considerable number of the F<sub>2</sub> generation. The distinctively Emmer characters must therefore have been carried chiefly in the 7 chromosomes which originally paired with the 7 *monococcum*.

Mather (1935) made a critical study of hybrids of *T. dicoccum* × *T. monococcum* and the parents. He found in addition to the presence of 3 to 7 bivalents and 6 to 12 univalents in the hybrids, the occurrence of 0 to 3 trivalents (1 to 2 being very common). These trivalents were either of the chain or occasionally of the rod ring type. The presence of multivalents in the parents of the hybrids he considered was an index of structural hybridity and the occurrence of unclean separation an index of inversions.

A study of the chiasma frequencies of the parents revealed a slight difference between *monococcum* and *dicoccum*; a marked reduction, however, was found in the hybrid compared with the parents.

The author came to the conclusion that the trivalents found were probably due to the association of two *dicoccum* chromosomes and one *monococcum*, whilst the bivalents were allosyndetic.

Tschermak (1930) crossed *T. villosum* (*Haynaldia villosa*) ( $2n = 14$ ) with *T. turgidum*, *T. durum* and *T. spelta*. The *durum* and *spelta* hybrids were sterile, but the hybrids with *turgidum* were fertile and intermediate in character. Cytological examination proved that they possessed 42 chromosomes, the chromosomes of both species in the diploid condition ( $14 + 28$ ). The reduction division was perfectly normal, the gametes having 21 chromosomes ( $7 + 14$ ).

According to Tschermak, no pairing of chromosomes took place in the F<sub>1</sub> generation, but the single chromosomes split and thus gave rise to a true diploid condition. (See also Tschermak-Seysenegg, 1933; van Berg, 1934, a and b.)

Further proof of the new hybrid's diploid nature has since been obtained by back-crossing with one of the two original parents (Tschermak-Seysenegg, 1930), and also by further cytological analysis (Berg, 1934, a and b).

As the fertile hybrid has been constant over several generations, it can be regarded as a new species, *T. turgido villosum*.

A hybrid which is stated to contain the genom of three different species has been described by Kostoff (1932). Hybrids of *T. dicoccum* × *T. monococcum* formed unreduced gametes with 21 chromosomes. When this was pollinated by *T. vulgare* plants were obtained with 42 chromosomes.\*

\* See also, Kostoff, D., 1936. Production expérimentale des Triticum polyploïdes: des tri-hybrides en agriculture. Rev. Bot. Appl. 16-249-264.

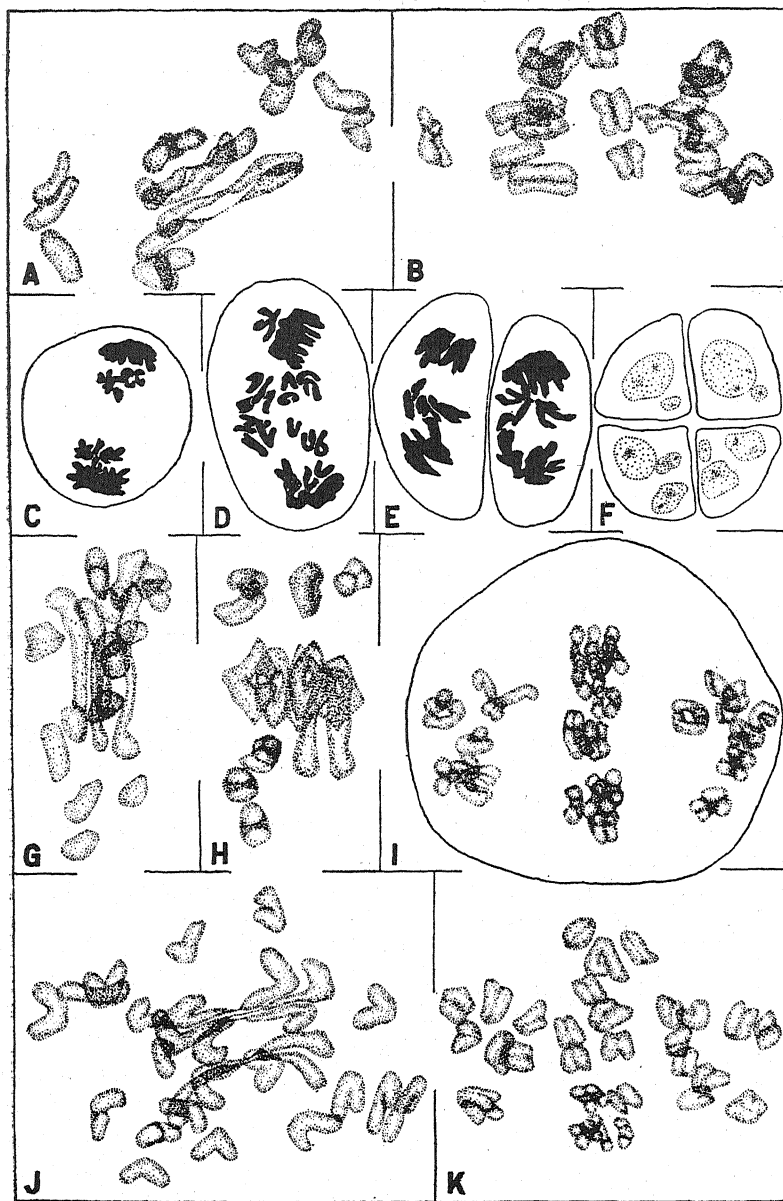


FIG. 55.

Chromosomes in *Triticum*  $\times$  *Triticum* hybrids: A, Heterotypic metaphase in *T. dicoccoides*  $\times$  *T. monococcum*; B, heterotypic anaphase in *T. dicoccoides*  $\times$  *T. monococcum*; C, late heterotypic anaphase in *T. dicoccoides*  $\times$  *T. monococcum*; D, heterotypic anaphase in *T. dicoccoides*  $\times$  *T. monococcum*; E, homotypic anaphase in *T. dicoccoides*  $\times$  *T. monococcum*; F, tetrad in *T. dicoccoides*  $\times$  *T. monococcum*; G, heterotypic metaphase in *T. polonicum*  $\times$  *T. monococcum*, showing four bivalents and two univalents in the plate region; H, heterotypic metaphase in *T. turgidum*  $\times$  *T. monococcum*; I, late heterotypic anaphase in *T. turgidum*  $\times$  *T. monococcum*; J, heterotypic metaphase in *T. compactum*  $\times$  *T. monococcum*; K, heterotypic anaphase in *T. compactum*  $\times$  *T. monococcum*. A, B, G–K, X 2,000; C–F, X 875. (After Longley and Sando.)

The situation that arises when members of Group I are hybridized with the single species of Group III has already been mentioned.

B. *Diploid* ( $n = 7$ ) by *Hexaploid* ( $n = 21$ ) *Species*. (*Tetraploid hybrids*).—The number of these crosses studied is fewer than in the above. Again, the cross is more readily performed if the seed parent has the higher chromosome count. (Bleier, 1928.) According to Percival the hybrids are sterile; Kihara and Nishiyama (1928) report them as weakly fertile.

The number of bivalents formed should be 7, but is consistently fewer. In *T. spelta* ( $21$ )  $\times$  *T. monococcum* ( $7$ ), Melburn and Thompson (1927) reported a range of 0 to 5, the pairing being loose; in *T. spelta* ( $21$ )  $\times$  *T. aegilopoides* ( $7$ ), Kihara and Nishiyama found 6 to 10 bivalents, with occasionally 1 or 2 trivalents; in *T. vulgare* ( $21$ )  $\times$  *T. monococcum* ( $7$ ) Bleier (1930) found only 0 to 5; and in *T. vulgare*  $\times$  *T. monococcum* and *T. compactum*  $\times$  *T. monococcum*, Longley and Sando (1930) reported 0 to 7. There appears to be a weaker homology here than in the triploid hybrids.

No study of the  $F_2$  generation appears to have been made.

C. *Tetraploid* ( $n = 14$ )  $\times$  *Hexaploid* ( $n = 21$ ) *Species*. (*Pentaploid hybrids*).—These crosses have been studied extensively (e.g., Kihara (1919), Sax (1922), Kihara (1924), Watkins (1924), Kihara and Nishiyama (1928), Aase (1930), Raum (1931), Wakar (1932), Kihara (1932), Hollingshead (1932), Wakar et al. (1932), Kihara et al. (1933), Wakar (1933), Kihara et al. (1935)). They exhibit a variable degree of intermediacy in the expression of the characters, are moderately fertile, with approximately 25 per cent. bad pollen, and failure to set grain in many flowers.

At the reduction division, the behaviour is almost uniform. The 35 chromosomes form 14 bivalents and 7 univalents; Sax (1922) reported a case of 9 univalents and Kihara and Nishiyama the rare occurrence of trivalents. In the heterotype division of the pollen mother-cell the bivalents separate normally; the univalents segregate at random and through lagging may arrive too late to be included in the daughter nuclei. In the homotype, the descendants of the bivalents again behave normally; the variable number of univalents once more segregate at random and some may for the second time fail to be included. The tetrad nuclei accordingly contain any number of chromosomes from 14 to 21.

The embryo-sac mother-cell divisions parallel those of the pollen mother-cells.

It is assumed that the univalent chromosomes belong to *Vulgare*, and that it is the same 7 that always remain unpaired. The 14 *Emmer* chromosomes must accordingly have definite homologies with 14 of the *vulgare*.

The  $F_2$  plants have any number of chromosomes from 28 to 42. These plants can be divided into two classes, on the basis of their chromosome combinations:

- a. Plants with 35 chromosomes (or less), having normally 14 bivalents + 0 to 7 univalents.
- b. Plants with more than 35 chromosomes, having the sum of the bivalents plus the univalents nearly always 21 (e.g., 16 bivalents + 5 univalents, or 20 bivalents + 1 univalent).

Plants belonging to both classes are more or less fertile and vigorous, and constitute Kihara's "fertile combinations." All other combinations are either not obtained or produce dwarf and sterile plants ("sterile combinations").

Further, the plants with fewer than 35 chromosomes give on selfing progeny with the same number of chromosomes or fewer ; by continued selfing, 14 bivalents are finally produced.

The plants with more than 35 chromosomes give rise to plants with the same or a greater number of chromosomes ; continued selfing thus gives ultimate forms with 21 bivalent-chromosomes. Accordingly the final result of the initial cross is the segregation of the original chromosome types. This is a direct consequence of the absence of the sterile combinations. (Kihara, 1919, 1921 ; Sax, 1923 ; Watkins, 1924 ; Kihara, 1924, etc.)

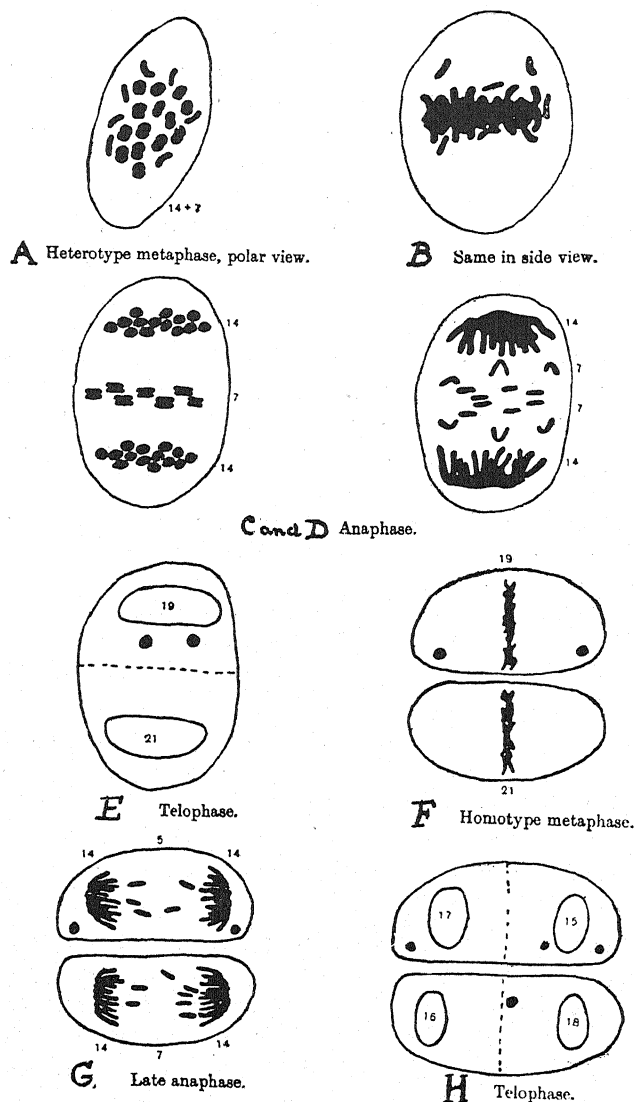


FIG. 56.

Reduction divisions in pentaploid wheat hybrids. Somewhat diagrammatic. (After Watkins.)

THE ABSENCE OF INTERMEDIATE COMBINATIONS IN PENTAPLOID HYBRIDS.—The causes of the absence of certain combinations have been studied by several investigators, and recently reviewed by Watkins (1930) and by Thompson (1934). Various aspects have also been discussed in connection with the incompatibility problem in several investigations.

Following (in part) Thompson (1934), the factors may be analysed under four main headings.

I. *Pre-gametic Effects* :—In this connection, the possibility that random segregation of the 7 unpaired chromosomes does not take place must be considered, (i.e., that the segregation of  $14 + 7$  or  $14 + 0$  is in some way more frequent).

In earlier papers, Thompson and Hollingshead (1927), Thompson and Cameron (1928), and Sax (1928) presented data which appeared to indicate that an excess of 28 chromosome plants occurred in the F<sub>2</sub> generations. Watkins (1930), in a critical survey of these papers, states that "there is either loss of chromosomes during early embryonic divisions or a heavier chromosome loss on the female side than on the male, as well as departure from random segregation on the female side." He concluded that the second interpretation is to be preferred.

In a more recent paper, Thompson and Cameron (1932) counted the chromosome numbers of the developing pollen in  $21 \times 14$  hybrids and found that all gametes were present in approximately the expected proportions. There was, however, a slight deficiency of gametes with intermediate numbers. The total effect of the absence of random segregation therefore appears to be but slight.

II. *Gametic Effects* :—a. *The Male Gametes*.—Although Kihara (1921) first assumed that all pollen combinations were functional, he later (1924) considered that selective sterility occurred. All other investigators have come to a similar conclusion. Watkins (1924, 1925) in particular has stressed its importance. "It seems fairly certain that in those plants with more than 35 chromosomes, there must be a favouring of 21-chromosome pollen grains at the expense of those with lower numbers. For plants with less than 35 chromosomes, where the expected proportion of sterile combinations is much smaller, the evidence is not so strong and elimination of gametes with 15 or 16 chromosomes in favour of the 14 may be less marked." (Watkins, 1930.)

On analysis the following situation has been found :—

1. *Death of Pollen Grains*.—In most instances about 10 to 15 per cent. of the pollen grains are empty.

2. *Retardation of Development*.—All pollen grains of the F<sub>1</sub> develop normally until the large vacuole is present. (Thompson and Armstrong, 1932.) Thereafter there is a definite tendency to retardation of development, accompanied by reduction in the amount of cytoplasm in the case of grains with intermediate numbers. Approximately 25 to 30 per cent. may exhibit this condition.

3. *Pollen Germination*.—Empty and defective grains are incapable of germination, and therefore only 60 to 70 per cent. of the grains have the potential capacity to germinate. Actually Watkins found only 5 to 30 per cent. of the pollen germinated, whilst Thompson and Armstrong (1932) state that only 5 to 15 per

cent. of the pollen in contact with the stigmas developed tubes. Accordingly a very large percentage of the grains potentially capable of germination fail to do so.

4. *Selective Fertilization*.—That selective fertilization may occur in wheat is now established. Thus Kihara (1932) found that when mixed pollen of durum and vulgare was applied to the stigmas of vulgare, the number of vulgare plants was 248 to 46 hybrids. When, however, durum was used as the seed parent, the number of non-hybrid to hybrid seeds obtained was approximately equal. In the case of the pentaploid hybrids, the results obtained would depend on whether the pollen grains with certain chromosome numbers are handicapped. Here the evidence is not conclusive.

Kihara *et al.* (1933) studied the progeny of  $F_1$  hybrids of *T. Polonicum*  $\times$  *T. spelta* and of *T. vulgare*  $\times$  *T. durum* when pollinated with their respective hexaploid and tetraploid parents. In both cases the tetraploid parental pollen gave rise to hybrids with predominantly low chromosome numbers, the maxima being 16 and 14 respectively. As a consequence the tetraploid pollen (14n) must have fertilized eggs mainly with 14 to 17 chromosomes. On the other hand, when the hexaploid parental pollen was used, the hybrids had higher chromosome numbers, the maxima being 18 and 19. Here the hexaploid pollen (21n) must have been most effective on 18 to 21 chromosome eggs.

When the different species were used as seed parents and the  $F_1$  hybrids as pollen parents, 14 chromosome pollen functioned almost exclusively on the tetraploid female (Emmer); both 14 and 21 chromosome pollen, with a slight excess of 21, on the hexaploid parent (Vulgare).

b. *The Female Gametes*.—Sax (1922) was of the opinion that failure to set grain was due to non-functional eggs, possibly those with 17 or 18 chromosomes. Kihara (1924) first attributed failure to the absorption of embryos with sterile combinations of chromosomes. Later (1932, 1933), he concluded that very little absorption could take place. In a microscopical study, he found only 2 per cent. of the eggs had degenerated, whilst 57 per cent. were healthy but unfertilized and 41 per cent. contained embryos. Watkins (1925) concluded that most of the eggs are functional but fail to be fertilized by their own pollen. He conceded, however, that it was possible, especially in the more sterile plants, that some eggs might be non-functional and that in some cases embryo-absorption might occur. Neither supposition did he regard as proved.

III. *Endosperm Effects*.—In reciprocal crosses in wheat, the relation between the embryo, the endosperm and the mother plant alters. In the Emmer group, the embryo has 28 chromosomes, the endosperm 42 (14 + 14 + 14) and the mother plant 28. In Vulgare, the position is 42 : 56 : 42. If the varieties of these species are crossed, the number of chromosomes in the endosperm will vary in relation to the species employed as the seed parent. Thus in the cross ♀ 42  $\times$  ♂ 28, the endosperm will be 21 + 21 + 14 = 56 (8n); on the other hand, ♀ 28  $\times$  ♂ 42 will give an endosperm 14 + 14 + 21 = 49 (7n). Similarly, the chromosome number of the mother plant will vary.

Cross.	Embryo.	Endosperm.	Mother Plant.
Vulgare ♀ $\times$ Emmer ♂	21 + 14 = 35 (5n)	21 + 21 + 14 = 56 (8n)	42 (6n).
Emmer ♀ $\times$ Vulgare ♂	14 + 21 = 35 (5n)	14 + 14 + 21 = 49 (7n)	28 (4n).

Expressing the position in terms of the chromosome sets, the position is as follows. If A, B and C represent the three sets of 7 chromosomes in a *Vulgare*, and a'b' the two sets of 7 chromosomes in an *Emmer*, then in a cross hexaploid

♀ × tetraploid ♂, the embryo is  $\begin{Bmatrix} ABC \\ a'b' \end{Bmatrix}$ , the endosperm is  $\begin{Bmatrix} ABC \\ ABC \\ a'b' \end{Bmatrix}$ , whilst the mother

plant is  $\begin{Bmatrix} ABC \\ ABC \end{Bmatrix}$ . In the reciprocal cross, the embryo is  $\begin{Bmatrix} a'b' \\ ABC \end{Bmatrix}$ , the endosperm

$\begin{Bmatrix} a'b' \\ a'b' \\ ABC \end{Bmatrix}$ , and the mother plant  $\begin{Bmatrix} a'b' \\ a'b' \end{Bmatrix}$ . These differences affect the development of

the seed. When *Vulgare* is the seed parent, the endosperm is reduced in size but otherwise normal and the germination good, but when *Emmer* is the seed parent, the grains are shrivelled and germination poor. The table on the following page gives the results obtained in all combinations of wheat species.

When the pentaploid hybrids are inter-pollinated the situation is still more complex. In any one embryo sac, the polar nuclei may be  $\begin{Bmatrix} AB \text{ plus } 0 \text{ to } 7Cs \\ AB \text{ plus } 0 \text{ to } 7cs \end{Bmatrix}$  to which the male nucleus may add either AB plus 0 to 7 Cs or a'b' plus 0 to 7 Cs: or the polar nuclei may be  $\begin{Bmatrix} a'b' \text{ plus } 0 \text{ to } 7Cs \\ a'b' \text{ plus } 0 \text{ to } 7cs \end{Bmatrix}$  to which again the male nucleus may add either AB plus 0 to 7 Cs or a'b' plus 0 to 7 Cs. As a consequence very many of the seeds may be shrivelled and show poor or no germination.

Watkins (1927, 1932) first stressed this relationship and its effects, emphasizing the quantitative relationship between endosperm and embryo that arises. Germination he believed was good if the extra chromosomes (the C or *Vulgare* chromosomes) were all diploid or triploid, but bad if some only were present in the haploid condition. Thompson (1930) and Thompson and Cameron (1928) extended the analysis farther. They pointed out that "the endosperm is plump when the extra *vulgare* (C) chromosomes are absent or diploid or triploid or nearly so. It is likely to be wrinkled or shrivelled when (a) haploid for all or many of the 7; (b) diploid or triploid for some only. Now such abnormal combinations tending to produce poor endosperm development must occur precisely in those seeds from which the missing chromosome types would have to develop." Thus, for example, a plant with 18" of chromosome would have to develop from a seed which had four of the extra *vulgare* chromosomes represented three times in its endosperm and the remaining three entirely absent. The endosperm of such a seed would abort. In this connection it should be noted that Kihara (1932) found that 2 to 3 days after pollination 41 per cent. of the embryo-sacs contained embryos but that later only 16 per cent. contained embryos. Consequently about a half aborted and of the remainder only about half germinated. These conditions indicate that the chromosome complement of the endosperm must be a very important factor in the non-appearance of many expected chromosome and genetic types, more especially in the F<sub>2</sub> generation.

Thompson (1932) has also stressed the importance of these results in practical breeding—"Special attention" he points out "should be given to the shrivelled seed. . . . The shrivelled seeds are just those in which the combinations of



characters desired by the breeders are likely to occur." Also, he draws attention to the practical importance of the back-cross. "By its use types can be obtained which would never appear in direct crosses." "In the back-cross a larger proportion of gametes, particularly the female ones, function."

Non-setting and poor germination of grain, however, have been explained on other grounds. Thus, Kihara and Nishiyama (1932) in a study of pentaploid *Avena* hybrids, came to the conclusion that differential development is due to different potencies of the male nuclei in activating the egg and the fusion nuclei. If the male nuclei have relatively higher numbers, this gives a higher "stimulus-strength," resulting in abnormal rapidity of cell division in endosperm and embryo,

TABLE XXII.

KERNEL PRODUCTION, GERMINATION AND RELATIVE ENDOSPERM PRODUCTION IN PURE SPECIES AND HYBRIDS OF WHEAT.

(After Wakakuwa.)

Cross.	K. prod. Act. No.	per cent.	Germ. Act. No.	per cent.	K. develop.
Eink. ( $n = 7$ ) ♀ × Eink. ( $n = 7$ ) ♂	32	80.00	28	87.50	A little small, plump or somewhat wrinkled.
Recip.	27	93.10	15	88.24	" "
Emmer $n = 14$ ♀ × Emmer $n = 14$ ♂	94	97.92	92	97.80	About normal.
Recip.	128	95.52	118	95.93	" "
Dinkel $n = 21$ ♀ × Dinkel $n = 21$ ♂	36	85.71	36	100.00	" "
Recip.	33	80.84	32	96.91	" "
Emmer $n = 14$ ♀ × Eink. $n = 7$ ♂	119	73.46	110	93.22	A little small, plump or somewhat wrinkled.
Recip.	118	81.38	88	74.58	Large or small, usually wrinkled.
Dinkel $n = 21$ ♀ × Eink. $n = 7$ ♂	81	62.31	46	56.79	Very small, usually wrinkled.
Recip.	56	71.79	0	0.00	Large, shrivelled.
Dinkel $n = 21$ ♀ × Emmer $n = 14$ ♂	113	71.07	108	98.18	Somewhat small, plump.
Recip.	222	95.28	136	61.26	Large, very wrinkled.

followed by degeneration. Inversely, if the male nuclei have the lower chromosome number, the "stimulus" is weak, growth is slow with degeneration of endosperm but subsequent reconstruction; the embryos may fail but some survive. (See pages 77-78.)

Müntzing (1933) developed a wider conception. Differential seed development was due to a change in the quantitative relationship between embryo : endosperm : mother, based fundamentally on the fact that alteration of chromosome mass influences cell size and probably also the physiological condition. Normally the chromosome relationship is 2 : 3 : 2, but in crosses this relationship alters with increase or decrease in chromosome number (mass).

More fundamentally, Kostoff (1929, 1930), basing his conclusions mainly on *Nicotiana* hybrids, suggested that certain of the inhibition phenomena manifested in the early development of embryo and endosperm in hybrids was comparable to the antigen-antibody reactions found in immunology. This suggestion was not well received, but more recent studies have indicated that maternal tissue may act harmoniously or inharmoniously on developing endosperm and embryo. This suggestion and the data accumulated in the course of intensive studies of *Nicotiana* hybrids, have now led East (1935) to advance the wide generalization that "the parent with the higher chromosome number presents broader possibilities for harmonious chemical reactions during early development if the embryo-sac machinery is controlled by the parent having the larger chromosome number." Thus the viewpoint becomes more holistic.\*

IV. *Zygotic Elimination*.—Kihara's evidence (1925) indicates that plants which die in the young stages or before completion of their development have sterile combinations of chromosomes.

Summarizing, it will be seen that the non-appearance of certain chromosome combinations must be due mainly to selective elimination of certain pollen combinations and endospermic effects. All other factors discussed apparently produce only minor deviations.

THE NATURE OF THE SEGREGATES.—As noted above, the subsequent generations of a pentaploid hybrid segregate into two classes—a diminishing group ranging in chromosome numbers from 34 to 28 and an ascending series eventually reverting to 42. In general, the diminishing segregants tend towards the Emmer type, whilst the ascending segregants move towards the Vulgare type. This conclusion seems justified by the investigations of Sax (1923), Sax and Gaines (1924), Kihara (1924), Thompson (1925), Watkins (1927), Tochunai and Kihara (1927). At the same time, it should be noted that new and even abnormal types may appear, and that there is an increase in the variability of many characters. Thus, Vavilov and Jakushkina (1925), in a study of crosses between *T. persicum* and varieties of the vulgare group, state that decrease and increase in the intensity of the characters, comparatively seldom observed in crosses within the limits of one genetical group of species, in this case becomes a frequent occurrence. They even regard the segregation as the "Naudin" or "disharmonious" type rather than as Mendelian.

In general, it may be said that the tendency is to have association between chromosome numbers and the type, *i.e.*, the mask in which the characters combine to form the group. Also, most investigators appear to accept the simple hypothesis

\* See also, footnote, page 78.

that the 7 unpaired additional chromosomes of the vulgare parent determine the differentiating characteristics of the vulgare forms. There is evidence, however, that this cannot be absolute.

Certain individual characters studied are apparently carried on the extra chromosomes. This seems to be the position as regards rust resistance. Thus a resistant  $28 \times$  susceptible 42, gives resistant 28 and susceptible 42 segregates. (Hayes, Parker and Kurtzweil, 1920; Thompson, 1925; Aamodt, 1927; Tochinai and Kihara, 1927.) Nevertheless, Thompson (1925) obtained 3 vulgare-like segregates which were resistant, though not so resistant as the durum parent.

In a factorial analysis, Watkins (1927 a) has studied the inheritance of the waxy and the waxless condition; also the differential characters among others of glume-keel, glume-thickness and ear-laxity (1927 b; 1928). The results are difficult to summarize, and the student should consult the original papers, more especially for the evidence upon which the conclusions are based (Watkins, 1927, a and b, 1928, 1930; Watkins and Cory, 1931).

In both the 28-chromosome group and the 42-chromosome group, there are three principal glume and rachis types, more or less parallel to one another.

#### A. 28-chromosome group.

1. *Persicum* type (seen in *T. Persicum*). Glumes round and very loose; rachis tough.
2. *Turgidum* type (seen in most *durums* and *turgidums*). Glumes loose, keeled; rachis tough.
3. *Dicoccum* type (seen in *dicoccum* and *dicoccoides*). Glumes keeled, tough, rachis brittle, breaking above the spikelet.

#### B. 42-chromosome group.

4. *Vulgare* type (seen in the great majority of *vulgares*). Glumes round, loose; rachis tough.
5. *Speltoid* type. Glumes keeled, tough; rachis tough, but ear lax.
6. *Spelta* type (seen in *T. Spelta*). Glumes keeled, very tough; rachis fragile, breaking below spikelet.

It is suggested that the glume and rachis characters of the three types of both groups are due to three factors,  $k$ ,  $K$ , and  $Ks$ , which form a series of multiple allelomorphs, or more probably three groups of closely linked factors. Thus, types 1, 2, and 3 of Group A are related to each other by the same factors as types 4, 5 and 6 of Group B. In *persicum*, however, the factors in the  $K$  group affecting ear density have probably undergone further modification. The differences between types 1, 2 and 3 of Group A and the corresponding types 4, 5 and 6 of Group B, are due to the extra chromosomes present in all the types of Group B. These chromosomes are believed to carry a factor  $K'$ , producing an effect corresponding to that produced by  $K$  and  $Ks$ .

The formulæ for the various types would accordingly read:

Group A: 28 chromosomes.

1. *Persicum* type =  $(kk) +$  some further change.
2. *Turgidum* type =  $(KK)$ .
3. *Dicoccum* type =  $(KsKs)$ .

Group B: 42 chromosomes.

4. *Vulgare* type  $(kk) K^1K^1$ .
5. *Speltoid* type  $(KK) K^1K^1$ .
6. *Spelt* type.  $(KsKs) K^1K^1$ .

If the above be true, it follows that in the two groups, owing to the presence of the extra chromosomes in Group B, the same series of factor changes—from

$k$  to  $K$  to  $Ks$ —may produce morphological differences “that are not quite parallel in the two groups, and produce types that do not appear, phenotypically, to be related by the same factors.”

In a further paper, Watkins and Cory (1931) have confirmed and extended the above results. In *Vulgare*  $\times$  *Turgidum* crosses, the inheritance of waxy and waxless foliage was followed in detail. Thus, if *Vulgare* = ( $ww$ )  $W'W'$  and *Turgidum* = ( $WW$ ), then the  $F_1$  = ( $Ww$ )  $W'$ , where  $w$  and  $W$  are carried by paired chromosomes and  $W'$  by unpaired chromosomes. It was found that pairing between  $W$  and  $w$  was the rule (allosyndetic):  $W'$  is only rarely paired.  $F_1 \text{♀} \times$  *Turgidum*  $\text{♂}$  should give ( $Ww$ ) and ( $Ww$ )  $W'$  plants, mostly with less than 35 chromosomes. They should segregate in ratios of 3 : 1 and 5 or 6 : 1 respectively and both ratios probably occurred. *Turgidum*  $\text{♀} \times F_1 \text{♂}$  should give ratios in  $F_3$  of both 3 : 1 and 5 : 1, the 5 : 1 ratios resulting from plants with shrivelled endosperm. This result was obtained. ( $Ww$ ) and ( $Ww$ )  $W'$  plants appeared to be formed in the expected ratios. The ( $Ww$ )  $W'$  plants segregating in a 5 : 1 ratio gave rise to plants with the constitution ( $w w$ )  $W'$  which segregated in ratios of about 1 waxy : 2 or 3 waxless. The progeny of ( $Ww$ )  $W'$  plants also gave rise to true waxy and true waxless plants in the expected proportions. Further crosses between  $F_1$  and *Vulgare* gave rise to plants with more than 35 chromosomes which were waxy and bred true to waxy, except for about 2 per cent. of sterile dwarfs (the expected waxless steriles) and about 0.3 per cent. of waxless fertile combinations. The latter were expected owing to occasional pairing of  $W'$  with  $w$  in a ( $ww$ )  $W'$  plant. Some families, however, gave rise to aberrant results, perhaps due to natural crossing.

Raum (1931, 1934) analysed several crosses between tetraploid and hexaploid wheats for such characters as density, tightness of glumes, brittleness of rachis and the awned condition.

As regards density, he postulated the presence of 4 genes, viz., the lengthening factors  $L_1$  and  $L_2$  (=  $A$  and  $B$ ); a compactum factor  $C$ , and a third lengthening factor,  $L$ . The  $C$  factor was present on all the tetraploid species employed, except *dicoccum* and *polonicum*. Its presence, however, is disguised by the  $L$  gene. In the hexaploid wheat,  $A$ ,  $B$ ,  $C$  and  $L$  are situated on the chromosomes which pair with those of the tetraploid.

The factor for tight glumes ( $S$ ) is believed to be present in all the wheats, but its expression is inhibited by a factor ( $H$ ) which may be present on one of the tetraploid chromosome groups and also on one of the extra groups in the hexaploids. Hence the following genotypes in the *vulgare* group would have tight glumes:— $SShh$  ( $hh$ );  $SSHH$  ( $hh$ )  $H$ , apparently due to greater potency of the genes on the extra chromosomes, and  $SShh$  (—); and the following loose glumes:— $SSHH$  ( $HH$ ),  $SShh$  ( $HH$ ) and  $SSHH$  (—). The above formulæ alone, however, did not explain the results, and mutation of ( $H$ ) to ( $h$ ) and interchange of segments were postulated to occur.

Brittleness was found to be inherited in a similar manner, the factors being  $B$  (brittle), present in all wheats, and  $Hb$  (inhibiting), present in all non-brittle types.

Summarizing the whole situation, it may be said that :—

1. Some characters are transferable from one species to another.
2. New characters may appear, and the variation of the old characters may be extended.
3. Many characters segregate in groups, depending probably on close linkage. This linkage may occasionally be broken.
4. Aberrant forms, sometimes with unexpected chromosome numbers, may be produced.
5. Close association between chromosome number and type has been clearly established.

### III. INTER-GENERIC CROSSES.

A. WITH *AEGILOPS* SPP.—The genus *Aegilops* is closely related to *Triticum*. Twelve species, indigenous to Southern Europe and Western Asia as far as Afghanistan and Turkestan, were described by Ascherson and Graebner. (*Synopsis der Mittel-Europäischen Flora*, Bot. 2, Abt. 1, p. 703–714.) Since then further species have been described, 20 being recognized by Zhukosky (1928) and 22 by Eig (1929).\*

Vavilov (1922) and Papova (1923) have emphasized the marked parallelism that exists in the variability of *Aegilops* as compared with *Triticum*. Further, *Aegilops* also constitutes a polyploid series, being divisible into diploid, tetraploid and hexaploid groups, with 7 as the fundamental haploid number (Schilman, 1923; Sorokina, 1928).

The two commonest species in Europe are *A. ovata* L., widely distributed along the Mediterranean region and extending into Syria and Transcaucasia; and *A. cylindrica* Host., extending from Italy through the Balkans to S. Russia and Asia Minor. Both species naturally cross with wheat and, as will be seen, the so-called *A. triticoides* is the hybrid of *A. ovata* with wheat pollen. Papova (1923) also reports the occurrence of hundreds of natural hybrids in Turkestan. Two of the groups analysed indicate that their parentage was *A. cylindrica* × *T. vulgare* and *A. crassa* × *T. vulgare*.

a. *Earlier studies of natural and artificial hybrids of Aegilops ovata* × *Triticum vulgare*.—Requien (1821–1824) collected specimens of a plant in the south of France, which he named *Aegilops triticoides* on account of its resemblance to wheat. It was later described as a new species by Bertolini in *Flora Italica*, Vol. 1, 1833.

The plant is generally completely sterile; it is tall and erect; the ears are bearded, cylindrical and carry 6 to 10 2-flowered spikelets. The glumes are somewhat flat and distinctly keeled with 1 to 2 awns. At maturity the ear disarticulates at the base.

Fabre (1838) cultivated *A. triticoides* for 20 years. Though at first sterile it became more and more fertile in succeeding generations, and with this increase in fertility it became more and more wheat-like. The later segregates were reported to be indistinguishable from the common wheats of the district. These results led Fabre and others to conclude that *A. ovata* was the progenitor of the cultivated wheats.

\* See also Eig, *Aegilops* L., *Pflanzenareale* 1936: 4: 43–50.

On the other hand, Godron (1854, 1856) produced evidence that *A. triticoides* was a naturally occurring hybrid, and in 1853 succeeded in producing the plant experimentally by crossing *A. ovata* with *T. vulgare* and *T. spelta*.

The work of Regel (1853) and others confirmed Godron's results, though the conclusions were for a time fiercely opposed by Jordan (1852, 1855, 1857).

The evidence accordingly indicates that Fabre's original plant was a hybrid. Its increasing fertility and more marked resemblance to wheat must have been due either to successive pollination by wind-borne wheat pollen, or to spontaneous self-fertility resulting from elimination of the *Aegilops* chromosomes in the reduction divisions.

b. *Later Studies of Aegilops-Triticum hybrids*.—In recent years, especially since Percival—mainly on morphological grounds—put forward the hypothesis that the *vulgare* wheats are complex hybrids derived from the inter-crossing of Emmer wheats with *Aegilops*, many *Triticum-Aegilops* hybrids have been secured, and some have been submitted to detailed cytological examination.

During the early period of these later investigations, the results obtained were rendered more difficult to interpret owing to the fact that knowledge of the cytogenetics of the *Aegilops*-parents was deficient. This period, however, was followed by a more critical analysis of the species of *Aegilops*, and there is now a better and an increasing understanding of the genus.

The species (over 20 in number) have been fully described. They constitute a polyploid series ( $X = 7$ , with diploid, tetraploid and hexaploid representatives), and exhibit marked parallelism to *Triticum* in the variability of certain of their characters. The karyology of the genus has been analysed in particular by Senjaninova—Korczagina (1932) and the genetical situation by Mieczynski (1931, 1933) and others.

## I. AEGILOPS-WHEAT DIPLOIDS.

Only a limited number of these hybrids have been obtained (Chizaki, 1932; Kihara et al., 1931, 1932; Oehler, 1933; Sando, 1935). In *A. speltoides*  $\times$  *T. monococcum* Chizaki found 2 to 3 bivalents (occasionally up to 7) and Kihara and Lilienfeld 2 to 4 bivalents (up to 7). Kihara therefore considers that the S. genom of *speltoides* has homology with the A of *monococcum*. Since *A. Aucheri* also contains S, a similar homology must be conceded.

The hybrids nevertheless are sterile.

## II. AEGILOPS-WHEAT TRIPLOIDS.

A considerable number of these hybrids have been obtained, and some have been examined cytologically (e.g., Bleier, 1927–28, 1930; Jenkins, 1929; Percival, 1930; Aase, 1930; Kihara and Lilienfeld, 1931–32; Laumont, 1932; Oehler, 1933, 1934; Kihara and Lilienfeld, 1935; Sando, 1935).

The pairing in these hybrids is on the whole lower than in wheat triploids, and according to Aase (1930), are almost exclusively of the open type. Percival also points out that the pairing is "telosyndetic," "each pair being joined end to end by a fine thread."

In *ovata*  $\times$  *monococcum*, the pairing found varied from 0 to 6 and 1 to 5. Jenkins (1929), however, found 4 to 10 bivalents (the majority with 7) in the cross *T. turgidum* v *buccale*  $\times$  *Ae. speltoides*.

The hybrids on the whole are sterile, but a few partially fertile have been found. Oehler (1934) obtained 12 plants in the  $F_2$  of a cross of *A. caudata* v *polyathera* ( $n = 7$ )  $\times$  *T. dicoccum* ( $n = 14$ ), which resembled the  $F_1$  hybrids, were fairly fertile and possessed 42 chromosomes ( $2n$ ).

### III. AEGILOPS-WHEAT TETRAPLOIDS.

A large number of tetraploid hybrids have been secured, especially between *A. ovata*, *cylindrica*, *triuncialis* and *ventricosa* with most of the Emmer series of wheats (Blaringhem, 1925, 1930; Percival, 1926, 1930; Bleier, 1927, 1928, 1930; Sax, 1927, 1928; Gaines and Aase, 1926; Kihara, 1929, 1931, 1932; Kagawa, 1928, 1929; Aase, 1930; Kihara and Lilienfeld, 1931, 1932, 1934, 1935; Katayama, 1931; Taylor and Leighty, 1931; Berg, 1931; Laumont, 1932, 1933 a and b; Oehler, 1933, 1934; Tschermak and Bleier, 1926; Tschermak, 1933; Tschermak-Seysenegg, 1933; Sando, 1935).

In all tetraploid hybrids, the chromosome pairing is low but tends to fluctuate. The bivalents formed are of the open type, referred to as "telosyndetic" by Percival (1930). Aase (1930) found occasional closed bivalents, and Kihara (1929) the presence of rare trivalents. Percival (1930) also noted that tripolar spindles may occur in *ovata* crosses, rarely in *cylindrica* crosses, very rarely in *triuncialis* crosses, but frequently in *ventricosa* crosses where a few quadripolar spindles may even be found. No adequate explanation of these differences has been advanced.

When wheat is employed as the seed parent, plump seed may be obtained but it often fails to germinate through a defective or absent embryo. Kagawa (1928), Kihara (1929), Bleier (1930), and others, however, have obtained fertile seed.

The  $F_1$  plants obtained are either sterile, partially sterile or slightly fertile. The genetical situation in a number of crosses has been analysed by Oehler (1933-34) and Buckinger (1933).

In 1926, Tschermak and Bleier obtained a fertile hybrid from *A. ovata*  $\times$  *T. dicoccoides* and later from *A. ovata*  $\times$  *T. durum* v *Arrascita Hildebrandtii*. The fertile segregates were found to possess 56 chromosomes—the complements of both parents (Bleier, 1928). Since then similar fertile Aegilotricums have been obtained from crossing *A. ovata* with *T. dicoccum* and *T. turgidum compactum*.

Kihara (1931) tested the chromosome composition of Aegilotricum by crossing it with *T. dicoccoides*, *T. spelta* and *A. ovata*. In the cross Aegilotricum  $\times$  *T. dicoccoides*,  $14^{II} + 14^I$  were found at reduction; in Aegilotricum  $\times$  *T. spelta*, 7 to  $14^{II}$ ; in Aegilotricum  $\times$  *A. ovata*  $14^{II} + 14^I$ . These results would indicate that Aegilotricum does in reality contain the 2 Emmer genomes A and B and also the *ovata* genomes D and E. Aegilotricum has since been crossed by von Berg (1931) with *turgidovillosum*.

The  $F_1$  hybrid possessed the sum of the complements of *Aegilops ovata* (14), *T. durum* (14), *T. turgidum* (14) and *T. villosum* (7). At reduction, there were  $14^{II} + 21^I$ . It would, therefore, seem that the durum and turgidum chromosomes paired, leaving the durum and villosum chromosomes unpaired. Nevertheless the hybrid was practically sterile owing to a failure of the anthers to open.

In 1925, Blaringhem obtained a tetraploid hybrid from *A. ventricosa*  $\times$  *T. turgidum*. Later, he back-crossed the hybrid successfully with the original

wheat parent. The offspring became progressively more fertile, and a number of lines were fixed which correspond in all their characters with *T. spelta*, but also exhibit a tough rachis and non-shedding of grain. Two of these are said to resemble known sections of *Spelta*; a third is claimed to represent a new form of *Spelta* (Blaringhem, 1931).

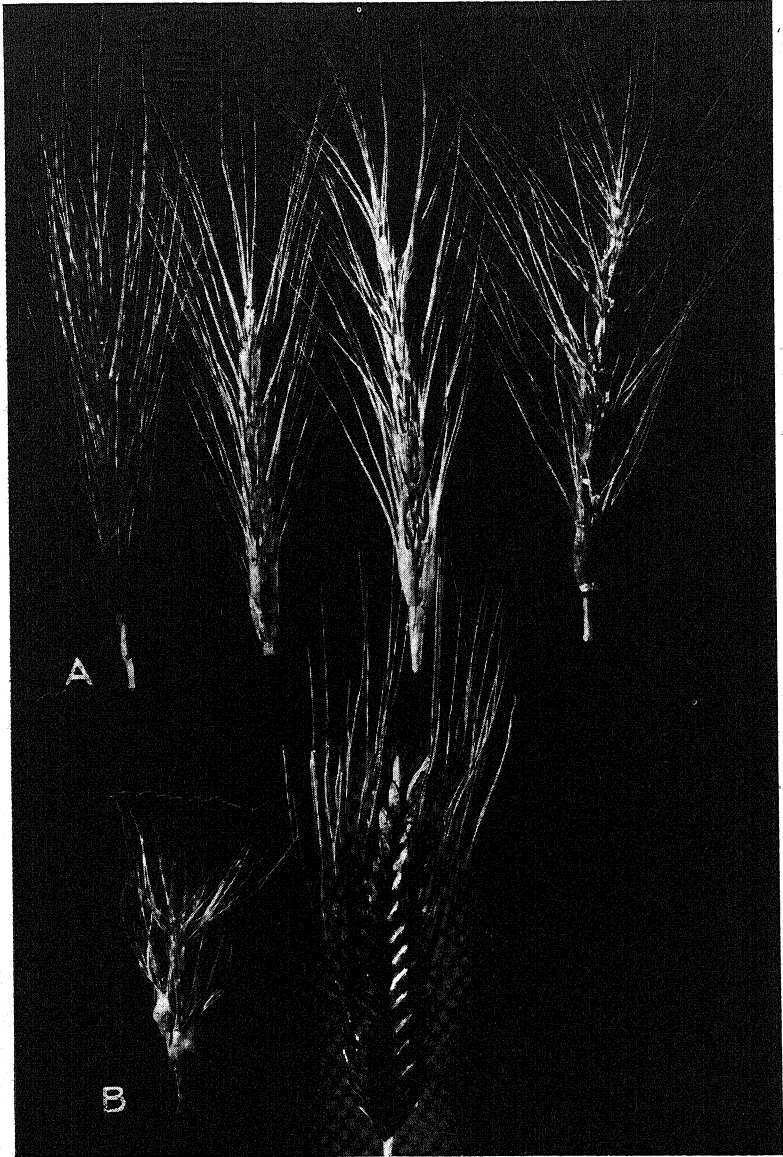


FIG. 57.

Hybrids of *Aegilops ovata* and *T. dicoccum*. A, (left to right),  $F_1$ ,  $F_2$ ,  $F_3$  and  $F_4$  progeny. B, the parents, *A. ovata* and *T. dicoccum*. (After Taylor and Leighty.)



A number of additional *Aegilotriticum* forms or partially fertile forms have also been obtained. Thus, Percival (1930) obtained an  $F_1$  hybrid with 28 chromosomes in the cross *A. ovata*  $\times$  *T. turgidum* v *mirabile*. It gave rise, however, to

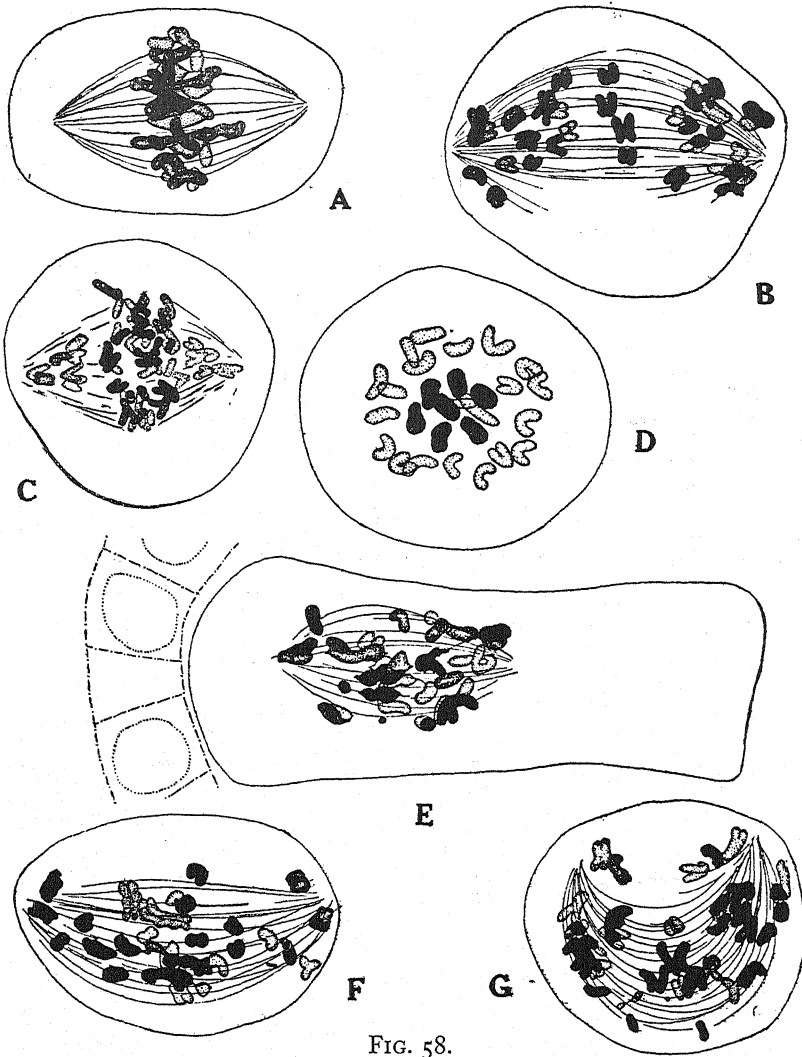


FIG. 58.

*Aegilops*-wheat pentaploids, first meiotic division. *Aegilops cylindrica* (14)  $\times$  *Triticum vulgare* (21), typical metaphase, side view, 14 univalents, 5 closed and 2 open bivalents. B, anaphase. All univalents and members of disjointed bivalents have split equationally and 4 univalents lying at the equatorial plate position will probably divide. C, same stage as B, but showing most of the univalents dividing.

D, *Ae. cylindrica*  $\times$  *T. spelta* (21), metaphase, polar view, 7 bivalents and 21 univalents; slightly more irregular than when *T. vulgare* is the wheat parent. E. This megaspore mother cell illustrates the irregular formation of univalents, bivalents and trivalents frequently observed in the spelt cross. F, metaphase, equational split occurring in all chromosomes. G, slightly irregular anaphase, some univalents dividing. X 1,300. (After Aase.)

3 grains on lateral ears from which practically 56 chromosome plants were obtained all exhibiting marked fertility. Taylor and Leighty (1931) segregated types which approximately maintained the characters of the  $F_1$  obtained by crossing *A. ovata*  $\times$  *T. durum*. Similar forms have been obtained by Longley and Sando (1926) and since by Sando (1935). Oehler (1933-34) also obtained 56 chromosome plants identical with  $F_1$  and fairly fertile from two varieties of *A. Triuncialis*  $\times$  *T. dicoccum atratum*. Finally, Laumont (1933 b) claims to have obtained in the  $F_3$  of *A. triuncialis*  $\times$  *T. durum*, a number of soft wheat forms, some sterile, some very fertile.

#### IV. AEGILOPS-WHEAT PENTAPLOIDS.

Many pentaploids hybrids have been made and studied (Bally, 1919; Emme, 1924; Sax and Sax, 1924; Percival, 1926 and 1930; Gaines and Aase, 1926; Bleier, 1927, 1928, 1930; Kagawa, 1928; Kihara, 1929, 1931; Aase, 1930; Oehler, 1933, 1934; Lilienfeld and Kihara, 1931, 1932, 1935).

In all the hybrids tested cytologically the compatibility, based on the number of bivalents present, is low except in *A. cylindrica*. Further, the bivalents found are of the open or "telosynedtic" type of Percival. Thus, in *A. ovata*  $\times$  *vulgare* types, 0 to 3, 4 and 5 bivalents may occur.

TABLE XXIII.

CHROMOSOME PAIRING IN SOME AEGILOPS-OVATA-VULGARE HYBRIDS.

Cross.		Chromosome numbers.		Chromosome pairing.	Authority.
Female.	Male.	Female.	Male.		
<i>A. ovata</i>	<i>T. vulgare</i>	14	21	0—few	Percival, 1926.
<i>A. ovata</i>	<i>T. vulgare</i>	14	21	0—3	Bleier, 1927-28.
<i>A. ovata</i>	<i>T. compactum</i>	14	21	0—3	Aase, 1930.
<i>A. ovata</i>	<i>T. spelta</i>	14	21	0—3	Aase, 1930.
<i>A. ovata</i>	<i>T. vulgare</i>	14	21	2—3	Percival, 1930.
<i>A. ovata</i>	<i>T. compactum</i>	14	21	2—3	Percival, 1930.
<i>A. ovata</i>	<i>T. spelta</i>	14	21	1—3	Percival, 1930.
<i>A. ovata</i>	<i>T. sphaerococum</i>	14	21	4	Percival, 1930.
<i>A. ovata</i>	<i>T. vulgare</i>	14	21	0—5	Kihara and Lilienfeld, 1931-32.
<i>T. vulgare</i>	<i>A. ovata</i>	21	14	—	Bally, 1919.
<i>T. vulgare</i>	<i>A. ovata</i>	21	14	—	Emme, 1924.

In triuncialis and crassa hybrids, the pairing is also low, varying from 0 to 7 and 0 to 6 respectively.

On the other hand the following table of the pairing in Aegilops-cylindrica-Vulgare hybrids clearly indicates that 7 bivalents are constantly produced and that even the reciprocal cross exhibits a similar tendency.

TABLE XXIV.

CHROMOSOME PAIRING IN SOME AEGILOPS-CYLINDRICA-VULGARE HYBRIDS.

Cross.		Chromosome numbers.		Chromosome pairing.	Authority.
Female.	Male.	Female.	Male.		
<i>A. cylindrica</i>	<i>T. vulgare</i>	14	21	5—7	Sax and Sax, 1924.
<i>A. cylindrica</i>	<i>T. vulgare</i>	14	21	7	Kagawa, 1928.
<i>A. cylindrica</i>	<i>T. spelta</i>	14	21	7	Bleier, 1927.
<i>A. cylindrica</i>	<i>T. spelta</i>	14	21	7	Bleier, 1930.
<i>A. cylindrica</i>	<i>T. vulgare</i> (Hussar)	14	21	7	Aase, 1930.
<i>A. cylindrica</i>	<i>T. vulgare</i> (Bluestem)	14	21	7	Aase, 1930.
<i>A. cylindrica</i>	<i>T. vulgare</i> (Martin)	14	21	7	Aase, 1930.
<i>A. cylindrica</i>	<i>T. vulgare</i>	14	21	7	Percival, 1930.
<i>A. cylindrica</i>	<i>T. compactum</i>	14	21	7	Percival, 1930.
<i>A. cylindrica</i>	<i>T. spelta</i>	14	21	7	Percival, 1930.
<i>A. cylindrica</i>	<i>T. vulgare</i>	14	21	5—9 (average 7)	Kihara, 1931.
<i>T. vulgare</i>	<i>T. cylindrica</i>	21	14	7	Gaines and Aase, 1926.
<i>T. vulgare</i> (Kobambano 3)	<i>A. cylindrica</i>	21	14	6—7 (M = 7)	Kagawa, 1928.
<i>T. vulgare</i> (U. A. C. No. 1)	<i>A. cylindrica</i>	21	14	6—7 (M = 7)	Kagawa, 1928.
<i>T. spelta</i> (alstroum)	<i>A. cylindrica</i>	21	14	4—8	Aase, 1930.

Percival (1930), in view of the above and the fact that the bivalents are of the parasyndetic type, came to the conclusion that it affords "very strong evidence that seven of the univalents of *A. cylindrica* have their exact homologues in the chromosome complex of hexaploid bread wheats."

The F<sub>1</sub> hybrids are sterile, but seeds have been obtained by Longley and Sando (1926) from *ovata* × *vulgare*, *triuncialis* × *compactum*, *triuncialis* × *spelta* and *triuncialis* × *vulgare*. Back-crossing of *ovata* × triticum hybrids resulted in 2.4 per cent. of seed; of *triuncialis* × triticum hybrids 2.7 per cent. The *Aegilops speltaeformis* plants so produced were partially self-fertile.

## V. AEGILOPS-WHEAT HEXAPLOIDS.

Such hybrids have been obtained and studied by Bleier (1930), Longley and Sando (1930), Oehler (1933, 1934) and Sando (1935). The compatibility varies from 0 to 7, but the occurrence of normal bivalents up to 7 in number indicates a fairly definite homology. According to Kihara and Lilienfeld (1935), crosses of *crassa* with *ovata* and *ventricosa* tend to show that one of the three *crassa* genomes is very similar to or homologous with one in *ovata* and in *ventricosa*. This common genome is probably the C. genom.

The hybrids are markedly sterile, but Oehler (1934) obtained three segregates from the cross *A. triaristata* v *attenuata* ( $n = 21$ ) × *T. vulgare* ( $n = 21$ ) which, though differing from the F<sub>1</sub>, were alike and gave constant progeny. Their chromosome number, however, was only 56, a total somewhat difficult to explain.

In attempting the solution of the relationship of Triticum and Aegilops, Schroeder (1931) has followed a new line of investigation by studying the anatomy of the rachis and the nature of the fracture. *T. aegilopoides* and *T. dicoccum* were found to be very similar. The former has the anatomical features which condition both the Emmer and the Spelt type of fracture. *T. durum* exhibited clear differences, whilst *T. turgidum* approached the durum type. *T. polonicum*, however, is again different. *T. vulgare* and *T. spelta* are anatomically very similar. In the genus Aegilops, *A. speltoides* came fairly close to the durum type. *A. sharonensis* and other species of *Platystachys* exhibited tendencies towards both types of fracture. *A. ventricosa* and *A. squarrosa* possessed the Spelt type of morphology, whilst *A. cylindrica* showed the Emmer type in the lower spikelets, the spelt type in the upper. In the section *Macrathera*, *A. caudata* had both types of fracture, whilst *A. uniaristata* and *A. comosa* (fracturing only at the basal spikelets and also allowing the whole ear to fall) possessed the Emmer fracture. All other species of this section exhibited the Emmer type below and the Spelt type above.

Schroeder regards *T. aegilopoides* as the most primitive form leading directly or indirectly to *dicoccoides*. Within the Emmer group the species form a series—*T. dicoccoides*—*T. dicoccum*—*T. durum*—*T. turgidum*. This group differs essentially from the vulgare group, where *T. vulgare* is believed to have been derived from *T. spelta*, independently of Emmer.

As regards Aegilops *A. sharonensis* is considered to be the most primitive, with *A. ovata* regarded as a separate phylum from a primitive ancestor. This species leads on then through *cylindrica* and *ventricosa* to *T. spelta* and so ultimately

to *vulgare*. In this hypothesis the Vulgare wheats originated from a spelt form derived from a brittle *Aegilops* of the ovata or ventricosa type.

B. TRITICUM-AGROPYRUM HYBRIDS.—The genus *Agropyrum*, closely related to *Triticum*, is widely distributed in Western and Eastern Europe, and includes about 20 species, mainly robust perennials found growing under a wide variety of soils and conditions.

According to Hillman (1910), a hybrid between *T. vulgare*  $\times$  *Agropyrum*

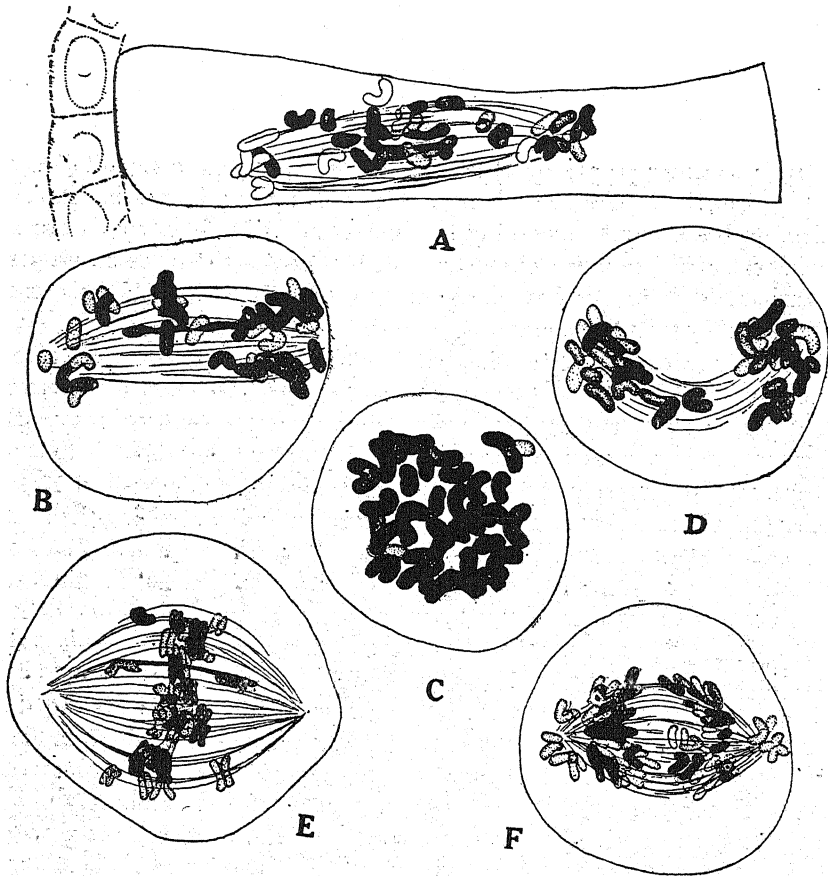


FIG. 59.

*Aegilops*-wheat pentaploid, first meiotic division. *Aegilops ovata* (14)  $\times$  *Triticum vulgare* (21). A, megaspore mother cell, 29 univalents and 3 open bivalents. The dispersal of the univalents over the elongated spindle is typical of the cross. (Unshaded chromosomes from upper section.) B, 33 univalents and 1 bivalent. C, the equatorial plate formation rarely observed in the cross. D, anaphase showing the random migration of the univalents to the two poles. Equational splitting is not evident. E, an anaphase quite the reverse of that in D, the equational splitting having occurred before components of the bivalents have separated. The univalents are arranged about as in C. F, a later stage of a state similar to E. The undivided chromosomes at the poles indicate that these were not at the equatorial plate when the splitting occurred, and hence prevented the complete non-reduction of univalents. X 1,300. (After Aase.)

*repens* was obtained by Fr. Strube. In 1933, Verushkine and Shechurdine reported the production of fertile wheat-couch grass hybrids between *T. vulgare* and *T. durum* with *Ag. intermedium* and *Ag. elongatum*. The percentage of fertilization obtained varied considerably, the success apparently depending on the suitability of the parents.

In the case of *T. vulgare*  $\times$  *intermedium* and *elongatum*, the seeds possessed clearly differentiated embryos, but as a rule abortive embryos; in *durum*  $\times$  *intermedium* and *elongatum*, the seed was generally normal with well-filled endosperm. 81.3 per cent. of germination was obtained in the case of *durum*  $\times$  *intermedium*; only 62.4 per cent. in the case of *vulgare*  $\times$  *intermedium*.

In all cases the F<sub>1</sub> plants were perennial and exhibited dominance of the couch



FIG. 60. Three Wheat Couch Grass Hybrids.

In each group the wheat parent is shown at the left, the F<sub>1</sub> hybrid in the centre and the Agropyrum parent at the right.

- A. Cross of the soft winter wheat lutescens 1,060/10 with *A. intermedium*. B. Cross of the hard spring wheat hordeiforme 432 with *A. intermedium*. C. Hard spring wheat hordeiforme 432  $\times$  *A. elongatum*. (After Verushkine and Shechurdine, by permission of the *Journal of Heredity*.)

grass characters. The majority were fully sterile, but a few partially self-fertile were obtained. By back-crossing the *vulgare* × intermedium hybrids, 10 per cent. of grain was obtained.

The same year, Tzitzin (1933) also obtained *Triticum-Agropyrum* hybrids with *Ag. glaucum*, *Ag. trichophorum*, *Ag. elongatum* and *Ag. junceum* (Verushkine says that the *Ag. glaucum* used must in reality have been *lolioides*).

Most of the work, however, was done with *glaucum* ( $2n = 42$ ) and *elongatum* ( $2n = 70$ ). Both species are stated to have crossed with ease with all species of wheat regardless of chromosome numbers. Reciprocal crosses were also obtained.

The  $F_1$  hybrids were mainly perennial but varied in pollen fertility very markedly. In the  $F_2$  generation they exhibited considerable segregation, showing more resemblance to wheat and even included types with *Aegilops* characteristics. Since the *elongatum* hybrids in particular possessed cold and drought resistance, combined with immunity to rust, smut, mildew and aphid, these hybrids are regarded as potentially of great economic importance.

In the  $F_1$  the hybrids had the expected chromosome numbers, i.e., *T. vulgare* ( $n = 21$ ) × *Ag. glaucum* ( $n = 21$ ) = 42; *T. vulgare* ( $n = 21$ ) × *Ag. elongatum* ( $n = 35$ ) = 56; *T. durum* ( $n = 14$ ) × *Ag. glaucum* ( $n = 21$ ) = 35; *T. durum* ( $n = 14$ ) × *Ag. elongatum* ( $n = 35$ ) = 49.

In a further paper, Verushkine (1935) reports that *Ag. elongatum*, *intermedium* and *trichophorum* have been crossed with species from all sections of *vulgare*. The hybrids of *vulgare* × *elongatum* proved the most fertile, many giving a normal setting of grain when self-pollinated. Some also gave from 80 to 100 per cent. grain when pollinated with wheat.

Subsequent generations from these hybrids have been secured (mainly by back-crossing with the wheat parent), even up to an  $F_7$  in one instance. Marked segregation in characters with an increase in the appearance of the wheat characters was found. There is also an increase in the number of annual forms. There indeed appears to be an ultimate segregation into three forms: true annual plants, true perennial plants and intermediates which react as annuals or perennials according to the conditions, e.g., they may behave as annuals in the field, as perennials in the greenhouse.

*Triticum-Agropyrum* hybrids have also been obtained by Wakar (1934) between *T. vulgare* and *T. durum* with *Ag. elongatum*. The hybrids, however, were completely sterile and resembled the *Agropyrum* parent.

The cytological situation in the hybrids is still obscure.

The species of *Agropyron* also fall into three groups with 7, 14 and 21 chromosomes. Certain species, however, appear to have strains with extra chromosomes:—e.g. *Ag. cristatum* with 7 and 14 chromosomes; *Ag. smithii* with 14 and 28; *Ag. elongatum* with 28 and 35.

Sapehin (1935) found 21 bivalents and only 7 univalents in the  $F_1$  of *T. vulgare* × *Ag. elongatum*. The race of *elongatum* used, however, had only 56 chromosomes, not 70. The hybrid *T. vulgare* × *Ag. glaucum* showed marked irregularity at meiosis. Though the chromosome number of the parents was the same, only two, occasionally three, bivalents occurred, and the formation of dyads and tetrads was equally irregular. Wakar (1935) has since analysed hybrids between *vulgare* and *durum* with *elongatum*. At metaphase there were

42 units, which appeared to consist of 14 bivalents and 28 univalents. In the case of the cross with *T. vulgare* × *Caesium* only 35 units were observed, 21 bivalents and 14 univalents. If the wheat genom be represented as A, B and D, and *Agropyrum* as A<sub>1</sub>, B<sub>1</sub>, D<sub>1</sub>, X<sub>1</sub> and X<sub>2</sub>, then the formula for the first cross can be assumed as AA<sub>1</sub> + BB<sub>1</sub> + D + D<sub>1</sub> + X<sub>1</sub> + X<sub>2</sub>; for the second cross as AA<sub>1</sub> + BB<sub>1</sub> + DD<sub>1</sub> + X<sub>1</sub> + X<sub>2</sub>.

In the case of the durum × elongatum hybrids, two types were also encountered. In the first type, there were 35 units, consisting of 14<sup>II</sup> and 21<sup>I</sup>; in the second, 28 units, consisting of 21<sup>II</sup> and 7<sup>I</sup>. The respective formulæ would therefore be :—for the first type, AA<sub>1</sub> + BB<sub>1</sub> + D<sub>1</sub> + X<sub>1</sub> + X<sub>2</sub>; for the second type, AA<sub>1</sub> + BB<sub>1</sub> + D<sub>1</sub> + X<sub>1</sub>X<sub>2</sub>.\*

C. WITH RYE. (See under Rye, page 222.)

**ABERRANT FORMS: SPELTIDS, COMPACTIDS, ETC.**—The commonest aberrant forms are the speltoids. In appearance they resemble *T. spelta*, but may be awnless or awned. Compactum and sub-compactum forms resembling *T. compactum* may also occur. All these types are genetically related, and may occur in the progeny of a single heterozygote. In addition, dwarf and giant forms are known, such as Vilmorin's "unfixable" dwarf, which always segregates into normal tall, unfixable dwarf and pigmy plants.

The speltoid form that is first noted in a supposedly pure line is generally a homozygous or true-breeding type, but the type that actually appears first is in nearly every instance heterozygous. Further, these types appear suddenly, either as "mutants" or chimeras in supposedly pure lines, or as segregates generally from vulgare hybrids. They have also occurred in the progeny of vulgare × turgidum hybrids (Watkins, 1930). That they are in origin "mutational," however, seems to be proved by the existence of chimeral forms. Thus Huskins found one wheat plant which bore three normal ears and two heterozygous beardless speltoid ears.

Speltoid and fatuoid forms were divided by Nilsson-Ehle (1921) into three series, A, B and C as follows :—

**Series A.** Heterozygous speltoid of Series A segregate typically into normals, heterozygous speltoids and homozygous speltoids in the ratio of 1 : 2 : 1, all segregates being of approximately equal vigour. The homozygous speltoids, however, may be deficient.

**Series B.** Speltoids of the B series when heterozygous give rise to 4 to 5 times as many heterozygotes as normals, accompanied by very few homozygous forms which are in general weak and sterile. Sub-compactum types may also be segregated.

**Series C.** Heterozygous C speltoids give rise to either more normals than heterozygotes or approximately equal numbers of both; the heterozygous segregates are generally few, but may vary in number from 2 to 20 per cent. of the total. As in the B forms, they are mostly weak and sterile, but the expression of both characteristics vary.

Although a "mutational" origin for these speltoids is indicated, there is lack of agreement as to the nature of the mutation, and it has also been argued that they

\* See also Vakar, Siberian Grain Res. Inst., Omsk 1935; Favorsky, Soc. Grain Farming Saratov, 1936: 6: 95-101; Sipkov, Bull. Appl. Bot. (1936) II (9): 357-60. Peto, Canad. J. Res. 14: Sect. e: 203-14, 1936.



arise from natural crossing. As in the case of fatuoids (see page 62) three hypotheses have been advanced.

1. That they are the product of natural crossing; 2. That they are due to gene mutation, and 3. That they are due to *quantitative* changes in the chromosome complement, *i.e.*, to chromosome aberrations.

1. THE NATURAL CROSSING HYPOTHESIS.—This hypothesis is the oldest and was first advanced mainly to explain the origin of Fatuoids. (See page 62.) It has only incidentally been advocated as an explanation of speltoids.

That speltoids do arise in the progeny of vulgare crosses and in certain wheat species crosses is now accepted. The speltoid characters, however, form a linked series, whereas all other characters segregate normally. Crossing, therefore, is probably never the direct cause of speltoid production. It is more probable that in a hybrid a situation is created which tends to induce the formation of the speltoid. (See under Fatuoid Oats, pages 63-66.)

2. THE GENE MUTATION HYPOTHESIS.—This concept was advocated by Nilsson-Ehle in a series of papers (1920, 1921, 1927) and subsequently by others. It has also been advanced in detail as an explanation for the origin of fatuoids (pages 68-71). The fact that on this explanation a group of genes must mutate simultaneously makes the conception difficult to accept.

3. THE CHROMOSOME ABERRATION HYPOTHESIS.—This explanation was first advanced by Winge in 1929. It is based upon the conception that *T. vulgare* is a polyploid species, with 3 sets of 7 chromosomes, the members of each set being similar but not identical. If the 7 pairs of chromosomes in the most primitive species be designated  $\frac{1, 2, 3, 4, 5, 6, 7}{1, 2, 3, 4, 5, 6, 7}$ , then in a vulgare wheat the constitution

would be  $\frac{1A, 1B, 1C, 2A, 2B, 2C, \text{etc.}}{1A, 1B, 1C, 2A, 2B, 2C, \text{etc.}}$ . There is also evidence that the factors concerned are situated on only one of these sets, and that the speltoid characters are hypostatic to the vulgare. The formula can, therefore, be abbreviated to  $\frac{ABC}{ABC}$

where C carries the vulgare characters and B the speltoid. Normally, A mates with A, B with B and C with C. Owing to their similarity, however, irregular conjugation may occur. Thus a conjugation A—A, B—C, C—B, could give a

gamete  $\frac{ABB}{ABC}$ , regarded by Winge as the heterozygous speltoid. The presence of the three B chromosomes would then permit the emergence of the group of speltoid characters. Such a plant would give rise to offspring with the constitution  $\frac{ABC}{ABC}$

(normal),  $\frac{ABB}{ABC}$  (heterozygous speltoid) and  $\frac{ABB}{ABB}$  (homozygous speltoid).

This hypothesis has since been extended and subsequently modified by Huskins, who found that quantitative change in the chromosome complement may be detected in all speltoids.

In the B series of speltoids, the simplest of the three types, Huskins (1927) and all subsequent investigators—(Vasiljev, 1929, Hakansson, 1930 b, 1931; Phipps and Gurney, 1933)—found 41 chromosomes, which at meiosis form 21

bivalents + 1 univalent ( $20'' + 1'$ ). Such a plant would be heterozygous with the formula  $\frac{ABo}{ABC}$ . Here the loss of the C chromosome carrying the normal wheat factors would permit the speltoid characters present on the B chromosome to be expressed.

Heterozygous B speltoids normally give rise to heterozygous progeny in the ratio of 5 : 1; they may also give rise to 10 : 1 and even 20 : 1 ratios. Further, they produce very few homozygous progeny, and when formed these are dwarf and sterile.

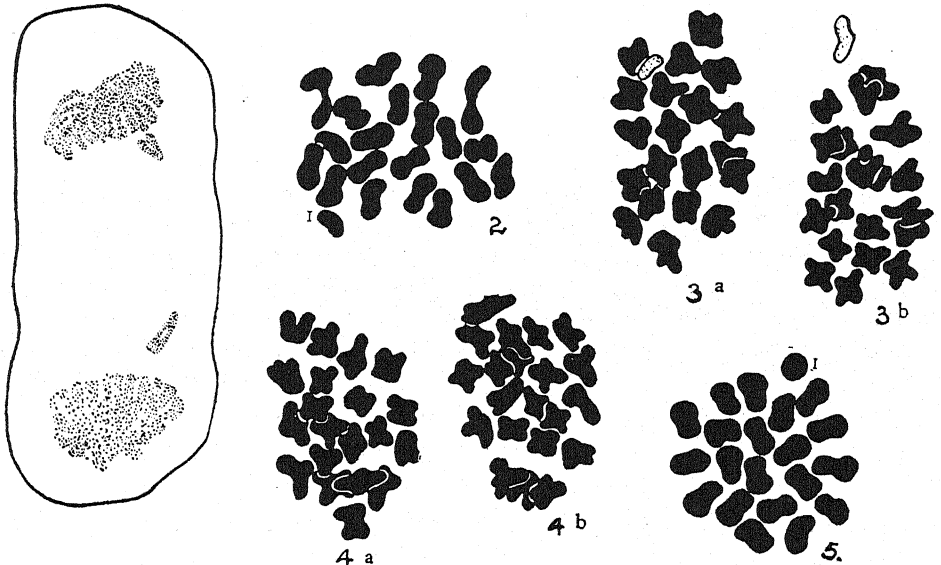


FIG. 61. "B" type Speltoids.

Heterotypic divisions showing 41 chromosomes ( $21'' + 1'$ ) in the heterozygotes. (After Huskins.)

The results are explicable on the chromosome situation. The plants with 41 chromosomes will form germ cells with either 20 or 21 chromosomes. Now crossing experiments have shown that the female germ cells with 20 or 21 chromosomes function, but that the male cells or pollen grains with other than the normal 21 chromosomes rarely effect fertilization. It follows that the ratio of 41 to 42 chromosome progeny, *i.e.*, of heterozygous to normal, must be practically the same as the ratio of 20 and 21 chromosome germ cells; but occasionally 20 chromosome pollen grains may function. If such a functional pollen grain fertilizes a 20-chromosome egg, a homozygous speltoid will result. These rare homozygous forms are dwarf and sterile. At meiosis they are found to be asynaptic. Instead of forming 20 bivalents, none of the chromosomes pair. The missing pair of C chromosomes must, therefore, have carried genes for normal pairing and division. Further, the absence of one of the C chromosomes and with it of one of the genes or one set of the genes for pairing and division must have some effect on the heterozygous plants, though not so drastically as on the 40-chromosome

homozygous plants. (Huskins, 1927, 1928, 1931, 1933; Huskins and Hearne, 1933; see also Nishiyama, 1933, on the C chromosome in fatuoids, pages 67-68).

The C series of speltoids are more complex. As noted above, the progeny of a heterozygous speltoid consist of normals and heterozygotes in about equal proportions, the homozygous speltoids present varying from 2 to 20 per cent. of the total according to the strain. These homozygous plants are not uniform; they vary in size from dwarfs to nearly normals and also in their sterility.

Cytological analysis of C strains first showed that they possessed 43 chromosomes in the heterozygotes, 44 in the homozygous and 42 in the normal segregates. The formula  $\frac{ABCB}{ABC}$  could, therefore, represent the heterozygous

plant,  $\frac{ABCB}{ABC}$  the homozygous plant. The fact that the heterozygous plants usually

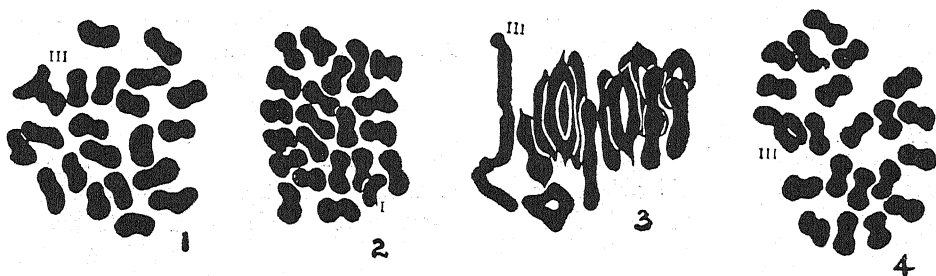


FIG. 62. Speltoids of "C" type.

Heterozygous forms showing 43 chromosomes. Nos. 1, 3 and 4 exhibit  $20'' + 1'''$ ; No. 2 has  $21'' + 1'$ . (After Huskins.)

exhibit 20 bivalents plus a trivalent and the homozygous segregates 20 bivalents plus a quadrivalent tends to support this conclusion. A similar situation was also found by Hakansson and Müntzing (1930). The segregation ratios obtained from the heterozygous plants are probably determined by the fact that more 21-chromosome gametes are formed than 22-chromosome gametes, modified in all probability by differential gametic variability and zygotic elimination.

In the light of recent research, however, the above explanation requires modification. There have been found sub-strains of the C series which, instead of having an extra chromosome, have the normal chromosome number with one chromosome deficient. They have lost about a half or more of the C chromosome; the missing part must thus have carried the vulgare complex of factors; the part retained must have borne the factors necessary for normal pairing (see Nishiyama for the constitution of the C chromosome in Fatuoids, pages 67-68).

The A series of speltoids are the most complex, but tend to occur more frequently than either the B or C series. They give rise typically to 1 : 2 : 1 ratios of normal, heterozygous and homozygous progeny, all the segregates being of approximately equal vigour. Some strains, however, give ratios of approximately 1 : 1 : 1, with a tendency for the homozygous progeny to be slightly less vigorous.

Huskins (1927) found that all segregates of series A had the normal number of chromosomes, but that the heterozygous forms were characterized by the presence of a trivalent and a univalent, the homozygous by a tetravalent. Adopting Winge's hypothesis, he assumed that in the heterozygous forms one of the C chromosomes carrying the normal factor was missing, and that this was compensated for by duplication of one of the B chromosomes carrying the hidden speltoid characters. The formula, therefore, was  $\frac{ABB}{ABC}$ , which could give segregates

$\frac{ABC}{ABC}$ ,  $\frac{ABB}{ABC}$ ,  $\frac{ABB}{ABB}$  in the ratio of 1 : 2 : 1. The genetic evidence, however, indicates that this explanation is not valid (Jones, 1935, and Nishiyama, 1933, on Fatuoids). A modification has therefore been advanced in alignment with recent cytological investigations. In all polyploid plants, occasional irregular pairing may take place. Thus a B-chromosome may occasionally pair with a C, rendering it possible for an exchange of segments to take place. Thus in a typical A series speltoid, instead of a whole C-chromosome being deleted and a whole B-chromosome

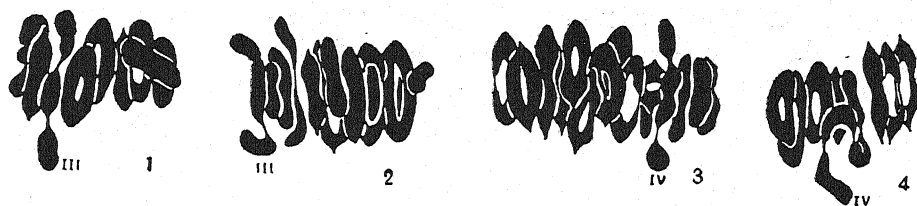


FIG. 63. "A" type Speltoids.

1 and 2, heterozygous speltoids with trivalents. 3 and 4, homozygous speltoids with tetravalents. (After Huskins.)

duplicated, it is far more probable that a portion of the C-chromosome has been deleted and a portion of the B-chromosome duplicated through interchange of segments. Groups of three and of four chromosomes must therefore be expected. Further, the amount of interchange could vary. Thus the A series which approach the C series in genetic type have a pair of chromosomes of very slightly unequal size, and have evidently lost a very small portion of the C-chromosome. (See under Fatuoids.)

It would accordingly appear that quantitative change in the chromosome complement is a satisfactory explanation of the mutative origin of the speltoids, more especially as regards the B and C types.

**INDUCED POLYPLOIDS.**—In the course of hybridization studies, many polyploid types have been obtained and some of these have been noted (see Kostoff, Rev. Bot. Appl. 16: 249-264, and also the Bibliography "*Experimental Production of Haploids and Polyploids*," Imp. Bur. Plant Genetics, Oct., 1936). In addition, polyploid types have been secured by the use of X-rays (see Sapehin, Piroda, No. 110: 221-224, 1934), and by temperature. Thus Dorsey (1936) obtained a series of polyploids by keeping the plants at 25° C between pollination and fertilization and then raising the temperature to 43° C for 20 to 30 minutes: e.g.,

*T. durum* var *marouani* ( $2n = 56$ ), *T. durum* var *Kubanka* ( $2n = 56$ ), *T. polonicum* Polish ( $2n = 56$ ), *T. vulgare*, var. *Honor* ( $2n = 84$ ).

ORIGIN OF WHEAT SPECIES.—As we have seen there are four groups of wheat, Einkorn, Emmer, Timopheevi and Vulgare, forming a polyploid series, whose basal chromosome number is seven. The groups are further distinguishable on morphological and serological characteristics, and three were so differentiated prior to their separation on the basis of their chromosome numbers. Further, the content of each group is very different. The Einkorn is strictly limited; the Emmer series consists of 7 (or 8) species, with certain of the species—and these the more valuable economically—exhibiting a wide range of more or less constant variability, the variates somewhat artificially classified as varieties: there is but one species known in Group III: the Vulgare series, though limited in the number of species to but four or five, far exceeds the others in its variability and consequently in the vast number of its varietal forms. Again this variability, as the Russian school has stressed—perhaps over-stressed—exhibits a marked parallelism.

To account for these facts is by no means easy, and several solutions have been offered.

A. WILD PROGENITORS.—a. *Of T. monococcum*.—The only related wild species is *T. aegilopoides*, Bal ex Körn, first described by Link from specimens found between Nauplia and Corinth in 1833. It is widely distributed from the Balkans to Syria and Transcaucasia. (Percival, 1921; Flaksberger, 1925, 1926 a.) Larionow (1909) discovered three varieties in the Balaklava district of the Crimea, and Drozdov (1923) mentions it as there forming a community with *Festuca ovina*, *Aegilops cylindrica*, *A. ovata* and others. According to Flaksberger (1925) it is found chiefly at heights of 700 metres or more above sea-level.

The relationship between this species and the cultivated *T. monococcum* is obvious. As Percival put it "In all morphological characters of the culm, ear, glumes, and grain there is little or no difference between the two, the only modification being a reduction in the hairs on the leaves and rachis."

A direct derivation of *T. monococcum* from one or other of the varieties of the wild species is accordingly accepted.

b. *Of T. dicoccum and the Emmer group*.—*T. dicoccoides*, Perc. was first noted by Körnicke as a portion of an ear among herbarium specimens of *Hordeum spontaneum* collected by Kotschy in 1853, at Rasheyya on Mount Hermon, Syria.

Aaronsohn (1906) rediscovered it at Rosh Pinar in Syria and later at Rasheyya and other centres. Its general distribution is now known to be from Palestine to Transcaucasia. That it is a wild species is evident from its natural habit among the crevices of limestone rocks at altitudes varying from 600 to 6,000 feet. Percival (1931) regards *T. dicoccoides* as the wild progenitor of *T. dicoccum*, the fragile-eared Indian-Abyssinian forms "exhibiting the closest resemblance to the prototype, possessing like the latter, easily disarticulated ears, short culms, yellow-green foliage, and the remarkable anatomical character of 4 to 6 vascular bundles in the coleoptile, as well as the early habit." This conclusion has been generally accepted although Flaksberger (1926 a) believes that *dicoccoides* resembles more

closely *Thaoudar* and *Aegilopoides* than *dicoccum* in spite of chromosome and other differences.

c. Of *T. Timopheevi*. This species is itself a wild form, becoming adventive.

d. Of *T. vulgare* and the *Vulgare group*.—No wild form in any way comparable to *T. vulgare* and its relatives has been discovered. Schulz and Flaksberger regarded *T. spelta* as a primitive form whose wild prototype, if it survives, is still unknown. Stapf, however, came to the conclusion that *A. cylindrica* could be so regarded. Percival's hypothesis will be considered later.

B. NATURAL DISTRIBUTION.—Vavilov, in a series of studies on the origin and distribution of cultivated plants (1926, 1927, 1931 and Vavilov and Bukinich, 1929), has found that wheat and other cultivated plants have definite centres of diversity. In these centres the greatest numbers of dominant types are to be found and as one leaves these centres the number decreases the farther one travels from the centre in question. These centres of diversity are assumed to be the centres of origin. On this basis, he has found in the case of wheat that there are three such centres.

(1) Asia Minor, (2) the Mediterranean basin and Abyssinia, (3) Afghanistan. In the first area the 14-chromosome wheats are most numerous; in the second the 28-chromosome wheats predominate; in the third, the vulgares. (42-chromosome wheats.)

The data as regards the 14-chromosome wheats is somewhat scanty but within the area both the wild type and the cultivated forms are widely found. In the Mediterranean-Abyssinian centre, all the cultivated forms of the Emmer group can be paralleled, and there exist many original and endemic forms. (Vavilov, 1931.) In the Afghanistan area (Persia, Afghanistan, Bokhara, Kashmir and Western India) there is an absence of Durums and Dicoccums, whereas the vulgare forms are numerous, again paralleling the cultivated forms of Europe. Further, endemic forms not known elsewhere are found, and Percival's *T. sphaerococcum* is known only from N. India. The new Spelt type, *T. macha*, also approaches in its distribution the Afghanistan area.

It is possible that these centres may not coincide precisely with the original centres of origin. Nevertheless, the main thesis appears to have been established. The geographical study of distribution has accordingly afforded collateral and independent proof that the division of the wheats into three main groups—previously based on morphological, cytological, genetical and serological grounds—is substantially correct. On the other hand, the problem of ultimate origin—especially the possibility of establishing a monophyletic origin, remains unsolved. Indeed it may well be that the new data has rendered a satisfactory solution even more difficult to obtain.

C. WINGE'S THEORY OF THE ORIGIN OF POLYPLOID SERIES.—This theory, first formulated by Winge in 1917 and afterwards extended, ascribes the origin of the polyploid series to chromosome doubling following hybridization.

Kihara and Ono (1926) have distinguished two categories of polyploidy—auto-polyploidy and allopolyploidy.

In auto-polyploidy the chromosome complement of the foundational species undergoes spontaneous doubling. In this manner, an Einkorn type ( $2n=14$ ) might have given rise to an Emmer type ( $2n=28$ ). If this were continued, the next

series would be octoploid, not hexaploid. Further, the chromosome complement of the Emmer type should then duplicate the complement of the original Einkorn type. So far as the wheats are concerned there is little to support the conception.

In allopolyploidy the production of a sterile hybrid precedes the doubling of the chromosome complement. Experimental evidence of this has been obtained in a number of cases; [e.g., in *Primula kewensis* ( $2n = 36$ ) resulting from the cross of *P. verticillata* ( $2n = 18$ )  $\times$  *P. floribunda* ( $2n = 18$ ); in Karpechenko's fertile hybrid resulting from the cross of *Raphanus sativus*  $\times$  *Brassica oleracea*, etc.] Applied to wheat, the situation, following Winge's original hypothesis, could be formulated according to the following scheme.

Stem Species.	A.	B.	C.
Chromosome numbers.	$2n = 14$	$2n = 14$	$2n = 14$
Gametes.	$7a$	$7b$	$7c$
Cross of A $\times$ B (sterile).	$7a + 7b$		
Doubling.	$7a^{11} + 7b^{11} \dots \dots \dots = n. \text{ sp. D.}$		
	$2n = 28$		
Gametes of D.	$7a + 7b$		$7c$
Cross of D $\times$ C (sterile).	$7a + 7b + 7c$		
Doubling.	$7a_{11} + 7b_{11} + 7c_{11} = n. \text{ sp. E.}$		
	$2n = 42$		
Gametes of E.	$7a + 7b + 7c$		

Three foundational species having the same chromosome numbers are here postulated. They may be either distinct species whose chromosomes are identical in number, but not strictly homologous, or forms of an original species whose chromosome complement have so diverged in course of time that strict homology is no longer possible. The cross between A and B results in a sterile hybrid due to their 2 chromosome complements, a and b, being incompatible. If the chromosomes do not pair, subsequent doubling of these could take place and every chromosome of each set would find a mate. The result would be a balanced hybrid D. If D then crossed with C, a sterile triploid would result. Further doubling of its chromosome sets would result in a form E with the formula  $7a + 7b + 7c$ . In spite of the difficulties, no better theoretical explanation of the problem of the origin of the polyploid wheats has as yet been advanced. Many recent hypotheses are in principle only an attempt to render this situation more concrete.

Percival's hypothesis (first formulated on morphological grounds in 1921) invokes the aid of hybridization to explain the origin of the hexaploid wheats only, although 3 stem species are involved. His argument, however, may fittingly be outlined here for all the species.

Series 1. Small Spelt, *T. monococcum*. Percival derives from *T. aegilopoides*. This fact has already been noted.

Series 2. The prototype is here *T. dicoccoides* ( $n = 14$ ). From it arose the

cultivated Emmers (*T. dicoccum*), the fragile eared Indo-Abyssinian forms being regarded as nearest the original; the European forms being probably later mutations.

The Macaroni or Durum wheats show affinities with both *T. dicoccoides* and *T. dicoccum*. They are regarded as mutations derived either directly from *T. dicoccoides*, or indirectly through *T. dicoccum*. The European Durums probably derive their characters from the European group of *T. dicoccum*.

Polish wheat (*T. Polonicum*) is regarded as a mutant from *T. durum*.

Rivet wheat (*T. turgidum*), however, is considered to be of hybrid origin, through the crossing of the tall European *T. dicoccum* × *T. compactum* (club wheat) or a dense-eared *T. vulgare*.

Egyptian Cone (*T. pyramidale*) is treated as an endemic dense-eared mutation from the Abyssinian form of *T. dicoccum*.

Series 4. Bread Wheats. Percival points out that the whole of this series differs from the Emmers in the following characteristics.

1. The presence of a long line of hairs on the crest of the longitudinal ridges of the young leaf with shorter hairs or no hairs on the sides.
2. Thin-walled hollow stems.
3. The tough non-disarticulating rachis.
4. The round back and absence of keel on the lower part of the glume in the majority.
5. The comparatively short awn of the fully-bearded types and the occurrence of semi-bearded types.

On the other hand he states that certain species of Aegilops, including *Aegilops ovata* and *Aegilops cylindrica*, possess all these characters. Percival accordingly regards this series as "a vast hybrid group" produced by the crossing of *T. dicoccoides* and its descendants with *A. ovata* and *A. cylindrica*. He claims that the extraordinary variability shown in the series and the evidence obtainable from artificial crosses support the contention.

As regards Table XXV it should be noted that hybridization is not invoked to explain the origin of the Einkorn and the Emmer series. *T. aegilopoides* and *T. dicoccoides* are accepted as primitive stem forms. On the other hand a hybrid origin is postulated for the whole of the vulgare series. This concept and the possible ancestry for the other groups will be considered in the following section.

D. CYTO-GENETIC EVIDENCE ON THE ORIGIN OF WHEAT.—*Analysis of the pure species.*—1. *T. monococcum* is generally accepted as akin to the primitive stock, and nearly related to the wild *T. aegilopoides*. The chromosome complement has been studied in some detail (Kagawa, 1927, 1929 a, 1929 b), and more recently the haploid by Kihara and Katayama (1933), Camara (1934) and Katayama (1935). (See Figs. 49 (1); 50 (a); 51 (d and e).) Darlington (1931) has calculated the total number of chiasmata and the number that are terminal. (See Fig. 52.)

The 7 chromosomes are usually regarded as basic, though forms have been noted in which 2 univalents may occur (Mather, l.c.), and in the haploid, Kihara and Katayama (l.c.) and Katayama (l.c.) have met with an occasional bivalent. The 7 chromosomes may be grouped into five types (Kagawa, 1927; Camara, 1934) and according to Camara (1935) four new additional types are very frequently



TABLE XXV.  
RELATIONSHIP OF THE RACES OF WHEAT.  
(After Percival.)

## Series I.

*T. aegilopoides* . . . . . *T. monococcum*.

## Series II.

<i>T. dicoccoides</i>	{	<i>T. orientale</i>	{	<i>T. durum</i> .	
		<i>T. dicoccum</i>		<i>T. dicoccum</i> Indo-Abyssinian	<i>T. pyramidale</i> .
				<i>T. dicoccum</i> European	<i>T. durum</i> . . <i>T. Polonicum</i> .
				<i>T. turgidum</i> .	

## Series IV (= III).

<i>T. dicoccoides</i>  ( <i>T. dicoccum</i> )  ( <i>T. durum</i> )	{	by	{	<i>Aegilops cylindrica</i>	{	<i>T. vulgare</i> .
				and		<i>T. spelta</i> .
				<i>Aegilops ovata</i>		<i>T. compactum</i> .
						<i>T. sphaerococcum</i> .

encountered in irradiated material. These additional chromosomes, the product of fragmentation and interchange, together with the original series, are claimed to parallel all the chromosome types characteristic of *T. dicoccum* (4n).

2. The additional pairs of chromosomes in Emmer wheat form a series of eleven types, four of which appear to differ from those of monococcum. (Kagawa.)

In Fig. 53 the bivalent chromosomes at metaphase are shown with the total number of chiasmata and the terminalization in two of the species. (Darlington, 1931.)

In certain of the pure species univalents may occur but very rarely. Quadrivalents and other multivalents are also known but seem to occur sporadically. In the hybrids within the group, univalents also occur sporadically, due probably to chance failure in pairing. This, however, may not apply to hybrids between *T. dicoccoides* × *T. polonicum* and *T. dicoccoides* × *T. durum*, where 9 to 11 per cent. of the pollen may show 1 to 2 univalents, probably the result of slight difference in homology. (Hosano, 1935.) There is also a reduction in the number of chiasma in the hybrids compared with the parents (Darlington, 1931).

As regards multivalents, quadrivalents have been noted in practically all, the highest frequency found by Hosano (l.c) being 35 per cent. of the cells examined in the case of *dicoccum* by *dicoccoides*.

Apart, therefore, from gene differentiation in the chromosomes, it would appear that some of the A genomes have parts in common with those of the B.

The cultivated Emmer wheats are regarded as possessing a wild prototype

in *T. dicoccoides*. At the same time it should be noted that *dicoccum* shows certain definite relationships with *Thaoudar* and *Aegilopoides*. Various attempts have also been made to inter-relate the species (e.g. Percival, pages 338–341), but the problem is one of extreme difficulty.

The genetical situation in the tetraploid wheat is in general conformity with the concept of an allopolyploid ancestry.

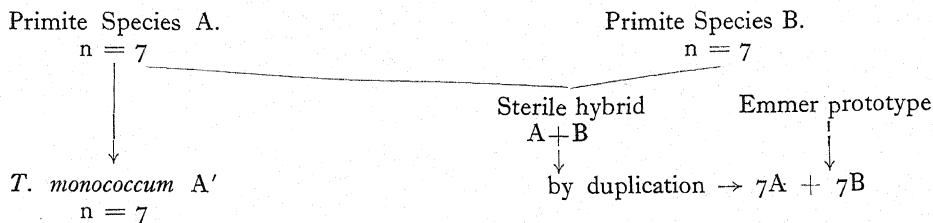
3. The hexaploid wheats have 21 chromosome pairs which may be grouped into approximately nine types (Kagawa, 1929, a and b). Certain of the types also do not appear to correspond to any of those in monococcums or Emmers. In crosses between the species, one or more pairs may fail to mate. Multiple associations may also form. (See Figs. 49 (10); 50 (b); 51 (K).)

The genetical analysis indicates that a very considerable number of characters are controlled by cumulative factors. This is to be expected in a polyploid species. Taking all the factors together, an allopolyploid origin is on the whole indicated.

ANALYSIS OF THE GROUP HYBRIDS.—The cyto-genetical analysis of the hybrids is also in general conformity with the allopolyploid hypothesis. In the first instance the genomes were represented as A, B and C, i.e., 7A in the monococcum group, 7A + 7B in the Emmer group and 7A + 7B + 7C in the vulgare group.

In the triploid hybrids, the pairing of the A's is variable, and often of the open type. The homology therefore seems weak. The A's of *Aegilopoides* appear to be nearer the A's of Emmer (at least *dicoccum*) than are the A's of *dicoccoides*. The converse may be true as regards *dicoccoides*. Mather's analysis of the reduction of chiasma frequency in the hybrids indicates that less than 0.7 per cent. of the total length of the monococcum chromosomes are homologues and pair with those of *dicoccum*.

Nevertheless, it seems reasonable to deduce that one ancestor of *dicoccum* was related to the ancestor of monococcum and that the second was akin but more distant.



The study of the tetraploid hybrids in general indicates that A genome is present in vulgare but that they are on the whole markedly differentiated.

The situation in pentaploid hybrids is fairly conclusive. The regular formation of 14 bivalents and 7 univalents indicates that the two sets of A and B chromosomes pair, whilst the 7C chromosomes are left unpaired. Occasional pairing, however, of C chromosomes with B chromosomes is also indicated.

That the A and B genomes of Emmer are present in vulgare appears a legitimate conclusion. The problem of the origin of the vulgare genome therefore remains.

Here, as already noted, the main interest has centred round the relationship of vulgare to species of *Aegilops*.

*Analysis of Aegilops-wheat hybrids.*—Percival's original hypothesis postulated either *A. cylindrica* or *A. ovata* as the second parent. Both *A. ovata* and *A. cylindrica*, however, are now known to possess 14 haploid chromosomes. Consequently the sterile hybrids obtained from the cross of Emmer wheats with either of these species is a tetraploid. A number of constant forms from these hybrids have nevertheless been obtained. The so-called Aegilotricum hybrids from Emmer wheats  $\times$  *A. ovata* proved to have 56 chromosomes, and appear to have no resemblance to any of the vulgare wheats.

Segregates from tetraploid hybrids, however, have now been obtained which do resemble vulgare types. Thus, Laumont (1931) states that he has obtained forms which resemble "soft wheats" in the  $F_3$  of the cross *A. triuncialis*  $\times$  *T. durum*, whilst Blaringham (1931) ultimately obtained spelt-like progeny by back-crossing with *T. turgidum* the hybrids of *A. ventricosa*  $\times$  *T. turgidum*.

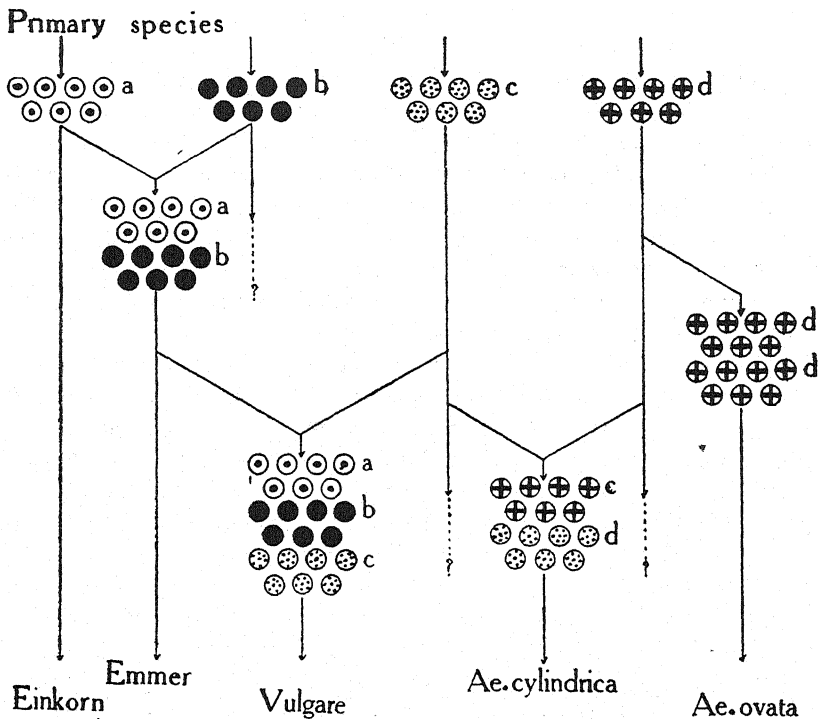


FIG. 64.

Diagram illustrating hypothetical relationships in wheat and Aegilops. The vulgare group is assumed to comprise descendents of a hybrid, of comparatively recent origin, between an emmer, a b, and a primary species, c; the emmer group the descendents of a hybrid, of comparatively ancient origin, between two primary species, a and b; the einkorn group the descendents of the primary species a. *Aegilops cylindrica* is a hybrid of comparatively recent origin; and has one parent, namely, primary species c, in common with vulgare wheat; and one parent, primary species d, in common with *Ae. ovata*. *Ae. ovata* shows some indications of being a true tetraploid; in which case it must be the tetraploid form of the primary species d. (After Aase.)

Up to the present no hexaploid progeny have been obtained from any of the triploid hybrids studied.

Nevertheless, support for the hypothesis has been obtained in the study of pentaploid hybrids. In the *Aegilops-cylindrica-vulgare* hybrids, several investigators have found that 7 bivalents regularly form. This has been interpreted as a pairing of the C chromosomes of the *vulgare* wheat with an homologous set in *cylindrica*.

Table XXVI indicates the homologies that have been postulated.

On their interpretation Gaines and Aase (1926) and later Aase (1930) advanced a hypothetical scheme of origins. Four stem species, A, B, C and D were postulated, each possessing 7 chromosomes. Primary species A probably gave rise directly to the Einkorn wheats. The Emmer wheats were regarded as of ancient lineage, the descendants of a hybrid between primary species A and primary species B. They accordingly contain the genomes a and b, which were duplicated in the original sterile hybrid. The homology of the a chromosomes in Einkorn and Emmers, however, has weakened in time.

The *vulgare* wheats arose from crosses between the Emmer wheats and primary species C which was akin to *Aegilops*. The sterile hybrids so formed, therefore, contained the genomes a + b + c, the C genom thus introducing certain *aegilops* characteristics. By duplication of the three sets, the hexaploid wheats arose.

The fact that 7 chromosomes of *A. cylindrica* exhibit regular pairing with 7 of the *vulgare* chromosomes was explained on the basis that *A. cylindrica* is a comparatively recent hybrid, between the primary species C and the primary species D. Accordingly, both *cylindrica* and the *vulgare* wheats contain the genom C. Further, it was suggested that *A. ovata* might be a tetraploid and hence derived (presumably by auto-polyploidy) from species D.\*

There are, however, many complications.

1. The genus *Aegilops* has not yet been studied in detail, and a much better cyto-genetical knowledge of the genus is a pre-requisite for a fuller understanding of the situation.

2. The cytological studies that have been conducted on the genera do not appear to favour the Percival hypothesis. Thus, Kagawa (1927, 1929 a and b) concluded that the *Triticum* species could not have been evolved by any reduplication of a basal chromosome set (*i.e.*, by auto-polyploidy) but that they might have been produced by the inter-crossing of ancestral forms having different chromosome contents. Comparison of the *vulgare* complement, however, with the complements of *A. cylindrica* and *A. ovata* gave little or no evidence of the presence in the *vulgare* complement of either the *cylindrica* or the *ovata* genomes.

Further, neither *A. cylindrica* nor *A. ovata* appeared to be auto-polyploids of *A. speltoides*, and the ratio of the longest and shortest chromosomes in that species (100 : 65) approximated to that of *T. monococcum* (100 : 68).

Senjaninova-Korczagina (1932), in a karyological study of *Aegilops*, found that *A. cylindrica* had a very definite karyotype and concluded that the species might be an allopolyploid of *A. bicornis* and *A. candata*. *A. ovata* was equally complex, containing a set of chromosomes resembling those of *A. umbellata* plus a set of

\* A modification and extension of this concept has recently been published by Miss Aase. See Aase, H.C. 1935. Bot. Rev. 1 : 467-496.



chromosomes not identified. Comparison of the two species *A. ovata* and *A. cylindrica* indicated that they differed markedly in their karyotypes. Also, when the karyotypes of *cylindrica* were compared with those of *vulgare*, no evidence whatsoever could be obtained of a set of the *cylindrica* chromosomes in the *vulgare* complement, thus confirming Kagawa's opinion.

ANALYSIS OF AGROPYRUM-WHEAT HYBRIDS.—A further complication has here been introduced. Although the analysis is very incomplete, it would appear that the A and B chromosomes of wheat may be homologous with two of the genomes in *Ag. elongatum* and that in certain instances the D genome of that species may pair with the D of *vulgare*. If the above be correct and we are justified in accepting pairing as an index of homology, it would seem to indicate that the relationship between *Agropyrum* and *Triticum* may be closer than that between *Triticum* and *Aegilops*. Also, *Ag. intermedium* has been successfully crossed with a number of species of *Aegilops* and with *Secale cereale*.

Summarizing the situation we may conclude :—

1. That there are at least three—probably four—groups of wheat species.
2. That they form an allopolyploid series.
3. That the members of the groups have different and practically discontinuous centres of diversity, probably corresponding to the centres of origin.
4. That wild species exist which are akin to the Einkorn and Emmer groups.
5. That there is homology, though variable, between the genomes of the species of the three groups.
6. That the *vulgare* wheats nevertheless show characteristics which are not present in Einkorn and Emmer.
7. That there is evidence—at present inconclusive—that certain species of *Aegilops* or ancestral forms of *Aegilops* may have contributed to the ancestry of *vulgare* wheats.
8. That the genera *Triticum*, *Aegilops*, *Agropyrum* (and very doubtfully *Secale*) possess genomes in common, probably indicating a common ancestry.

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## CHAPTER V

### RYE

THE rye plant (*Secale cereale*) is an annual under cultivation, but may at times show a tendency to a perennial habit. Thus, old rye stubble may sprout, and a field closely eaten down the first season may live to a second season.

**ROOTS.**—The seminal roots are few in number, one primary and three lateral, but variation in the number occurs. They are followed by the adventitious roots in whorls from the basal nodes. All are functional throughout the life of the plant, and a few may penetrate to very considerable depths.

According to Weaver (1926), the roots in a moist loam may have a lateral spread of 6 to 10 inches, a working depth of about 4 feet, and a maximum penetration of 5 feet. Environmental conditions markedly influence the habit. The table opposite indicates the position.

Compared with the other small-grained cereals, the roots of rye are in general more profusely branched. Thus, Nobbe (1869) compared wheat and rye when 55 days old, and found that the number of the roots of the first to the fourth order was 15,000 in rye against 10,700 in wheat, and the combined lengths of these roots 118 meters and 82 meters respectively.

**STEMS.**—The stems are erect and slender, tougher and longer than those of wheat, with an average of 4 to 6 nodes. A purplish pigment is developed. Varieties such as Rosen may be densely hairy for about 2 inches below the ear (hairy-necked types): all others are either glabrous, slightly spinous or tuberculate. Types with brittle stems are known, and according to Davidson et al. (1924) they have thinner cell walls, less lignin, lower crude fibre and higher pentosan content than normal plants. Hornburg (1929) states that brittle plants have also a lower percentage of silicic acid. The character behaves as a recessive.

**LEAVES.**—The sheaths are smooth, generally glabrous and tight; the ligule is very short and obtuse but may be absent in certain spring ryes; the auricles when present are white and narrow, tending to wither early; the blades are usually glabrous, narrow and linear. The pubescence of the leaf, however, may vary from the presence of small spines to small spines with hairs to dense velvety hairs.

Both leaves and stems of the majority of rye plants have a waxy covering. This character was found by H. Nilsson (1917) and by Berkner and Meyer (1927) to be a simple dominant. The recessive non-waxy condition is believed to be correlated with short straw, high density of the ear, earliness and susceptibility to rust.

Chlorophyll deficient types, though comparatively rare, are known. Nilsson-Ehle (1913) and Kalt (1916) were of the opinion that albino seedlings were the result of a loss mutation, and that they are due to hybridization. Davidson et al. (1924), however, found albino seedlings in in-bred strains.

TABLE XXVII.

VARIATIONS IN GROWTH OF RYE UNDER DIFFERENT TYPES OF CLIMATE AND SOIL.  
(Data from Weaver.)

Station.	Variety of crop.	Soil.	Height of tops, feet.	Working depth, feet.	Maximum depth, feet.
Short-grass plains :					
Yuma, Colo.    ..    ..	Winter.	Very fine sandy loam.	2·3	2·2	2·8
Flagler, Colo.    ..    ..	Winter.	Very fine sandy loam.	2·1	2·3	2·8
Burlington, Colo.    ..    ..	Winter.	Very fine sandy loam.	3·5	4·3	6·0
Limon, Colo.    ..    ..	Winter.	Very fine sandy loam.	2·3	2·0	2·0
Colby, Kan.    ..    ..	Winter.	Very fine sandy loam.	3·5	3·0	3·6
Averages    ..    ..			2·7	2·8	3·4
Mixed prairie :					
Yuma, Colo.    ..    ..	Winter.	Very fine sandy loam.	2·7	4·2	5·0
Colorado Springs, Colo.	Winter.	Sandy loam.	3·0	3·0	4·7
Mankato, Kan.    ..    ..	Winter.	Very fine sandy loam.	4·2	3·8	4·7
Averages    ..    ..			3·3	3·7	4·8
Tall-grass prairie :					
Central City, Nebr.    ..    ..	Winter.	Very sandy loam.	6·0	5·0	7·7
Central City, Nebr.    ..    ..	Winter.	Pure sand.	3·3	2·8	4·6
Lincoln, Nebr.    ..    ..	Winter.	Silt loam.	5·5	3·9	5·0
Lincoln, Nebr.    ..    ..	Winter (Rosen).	Silt loam.	6·5	3·7	5·0
Fairbury, Nebr.    ..    ..	Winter.	Clay loam.	4·5	4·7	5·2
Fairbury, Nebr.    ..    ..	Winter.	Alluvial.	3·8	3·9	4·2
Averages    ..    ..			4·9	4·0	5·3



**INFLORESCENCE.**—The inflorescence is a long uniform spike, but branched forms are known. The rachis is generally tough with 20 to 30 joints which are somewhat irregular in outline and densely hairy on the edges. Articulate types also occur. They may be (1) brittle to the base (e.g., var. *afghanicum*); (2) brittle in the upper two-thirds (e.g., var. *articulatum*); (3) brittle in the upper third only (var. *sub-articulatum*). Each joint carries a fertile spikelet, but there is no terminal spikelet. The total number of spikelets averages about 37.

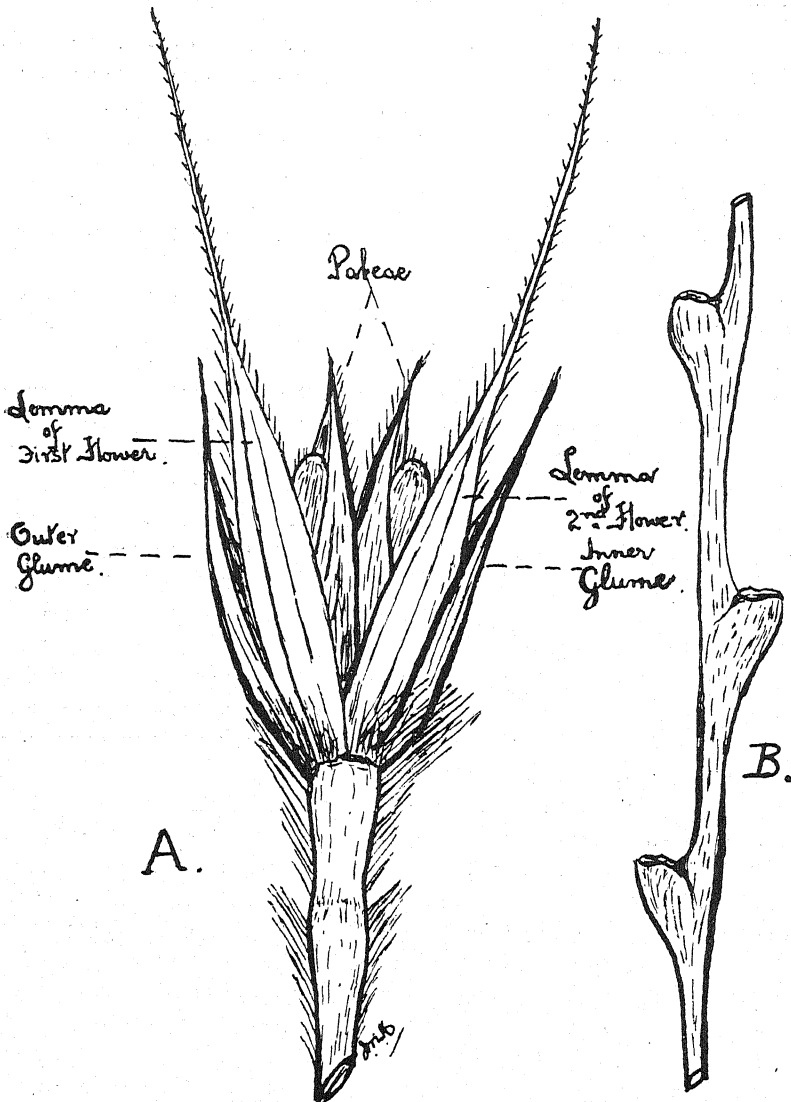


FIG. 65.

A. Spikelet of Rye at maturity.

B. Portion of rachis of ear of Rye.

**SPIKELET.**—Each spikelet has 2 narrow acuminate glumes. There are normally 3 florets, the 2 lower fertile, the third abortive. A type with the third floret fertile, however, is known. The lemma of each fertile flower is broad and keeled with long hairs on the keel, especially the upper third. It terminates in a long scabrid awn. The var. *muticum*, however, is practically awnless. The palea is thin, blunt and 2-keeled. There are 2 small membranous lodicules, ciliate on the upper margins, 3 stamens, and a single pistil, glabrous, slightly pubescent or strongly pubescent, with 2 feathery stigmas.

**ANTHESIS AND POLLINATION.**—The first flowers to open are those about one-third below the apex of the spike, anthesis proceeding thereafter both upwards and downwards. Flowering is said to commence between 5 and 6 a.m. and to continue throughout the morning until 9 to 11 a.m. Thereafter flowering is at a minimum until the evening when the percentage again tends to rise. The opening of each flower is rapid, and if pollination takes place immediately, the flower may be closed again within 30 minutes of the initial opening movement. Mechanical stimulation, such as rubbing, is said to induce the flowers to open.

Rye is cross-pollinated. This may be due to the fact that the stigmas project above the anthers which, as they emerge, tip over and dehisce the pollen outside of the flower.

Roemer (1931) found that the amount of cross-pollination decreased with the distance, and that in breeding experiments varieties should be separated by a distance of not less than 30 m. Cross-pollination was indeed observed, particularly in late flowering or self-sterile plants, up to a distance of 600 m.

The individual flowers of rye are generally self-sterile. (Ulrich, 1902 ; Fruwirth, 1909 and 1923.) There is, however, fertility between the flowers of a spike *inter se* (Obermeyer, 1916). Significant differences in self-sterility nevertheless occur, and the character is said to be inherited as a simple recessive (H. Nilsson, 1916, 1917, 1921 ; Brewbaker, 1926 ; Ageev, 1929). Strains which are completely self-sterile (Löwig, 1928) and completely self-fertile have been obtained. The preponderance of self-sterile strains in most cultivated varieties is regarded by Berg (1930) as due to selection and he believes that as a consequence the position might be reversed.

Von Rümker and Leidner (1914) found that cross-fertilized plants gave a higher yield than pure lines. Munerati (1924) compared self- and cross-fertilized plants which had been multiplied vegetatively and found that the yield of the crossed plants markedly exceeded that of the selfed. Ageev (1929) in-bred Wijaka rye and found that though degeneration was but slight in the first two generations, the germination capacity was low. Bredeman and Heuser (1931) found definite heterosis in the F<sub>1</sub> of crossed plants ; this was also marked in the F<sub>2</sub> ; in the F<sub>3</sub> and F<sub>4</sub> generations there was a definite falling off, but the yield was still equal to both or one of the original parents.

Antropov (1930) compared the sterility of the wild with the cultivated rye, and found greater self-sterility in the wild.

Berg (1928, 1930, 1931) has attempted the breeding of self-fertile forms, but the strains so far obtained have proved unsatisfactory. Nevertheless Brewbaker (1926) isolated self-fertile strains, which were as vigorous as cross-fertilized varieties,

and Duckart (1928) found 29 strains out of the progeny of 2,000 plants, which exhibited no degeneration from in-breeding after 9 years.

Partial sterility in rye is well known, and is apparently a heritable character (Plahn, 1916, 1927; Haupt, 1928). Leith, in 1925, found that the average sterility of the ears may equal a third of the total flowers. Koeslag (1927) showed that partial sterility is higher among so-called improved races, and that selection did not eliminate the characteristic.

The process of fertilization and the development of the grain in rye are essentially similar to that found in the other small-grained cereals.

**MATURE GRAIN.**—The ripe grain is free from the lemma and palea, and is longer, more slender, more sharply keeled, more pointed at the base and darker in colour than in wheat. The grains are also less uniform in shape, size and colour. In addition to the common grey-yellow colour of most varieties, a number of other colour forms are known. Thus, green, greenish-blue, yellow, deep blue, pale red, light brown, dark brown, and striped seeded varieties are known. According to von Rümker (1912, 1913), the pigments are located in the aleurone layer.

The internal structure is in general similar to that of wheat, but differs in detail.

I. **PERICARP.**—a. *Epidermis* (Epicarp).—The cells as in wheat are elongated, but the walls are thinner and less beaded. The hairs also have thinner walls and broader lumens with the tips more rounded.

b. *Parenchyma* (Mesocarp).—This is reduced to a single layer of cells with medium unbeaded or very faintly beaded walls.

c. *Cross Cells*.—This layer crosses the outer layers at right angles. Its component cells are symmetrically arranged side by side; the end walls are usually swollen and rounded, leaving small inter-cellular spaces; the side walls are somewhat thin and porous.

d. *Tube Cells*.—As in wheat but fewer in number.

The seed coat proper (Testa) and the nucellar epidermis (Perisperm) are so reduced that they are hardly distinguishable.

II. **ENDOSPERM.**—a. *Aleurone*.—There is a single layer of aleurone cells, somewhat irregular in outline when viewed from above.

b. *Parenchyma*.—This layer of thin-walled cells contains both starch and protein. The starch grains are of two types—large round grains often showing concentric rings and fissures and much smaller rounded or angular grains. Gluten is present in the protein and, as a consequence, bread may be made from rye flour. The protein content of the grain is from 6 to 12 per cent. and the starch content is higher than in wheat.

III. **EMBRYO.**—The structure of the embryo is similar to that of wheat.

**CHROMOSOME NUMBERS.**—Nemec (1910) reported 12 as the diploid chromosome number in rye, and Spilman believed that the haploid number was 6. Nakao (1911) gave the haploid number as 8. In 1918, Sakamura definitely established the numbers as 7 and 14 respectively. His results have since been verified by several investigators (Ferrand, 1923; Kihara, 1924; Nikolaewa, 1924; Gotoh, 1924; Stolze, 1924; Belling, 1925; Aase and Powers, 1926; Thompson, 1926; Longley and Sando, 1930).

Nevertheless, Kihara (1924) and Gotoh (1924) discovered plants identical in external appearance, some possessing 7 chromosomes, others 8. Gotoh (l.c.) also measured the chromosomes of the 7- and 8-chromosome plants and found the sum of both to be identical. He concluded that the additional chromosome was due to fragmentation, a conclusion supported by Belling.

On this basis, a 7-chromosome plant would have a constitution represented by  $(6 + 1k) = 7$ ; an 8-chromosome plant  $(6 + 1 + k) = 8$ . Further, the 1-chromosome is the larger segment and behaves normally: the  $k$  segment is much smaller and has a sub-terminal attachment dividing it into two arms in about the proportion of 1 to 7.

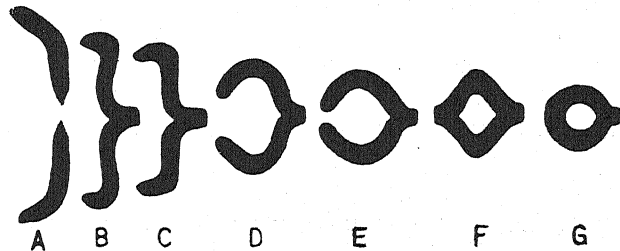


FIG. 66. Characteristic shapes of individual chromosomes in rye. (After Longley and Sando.)

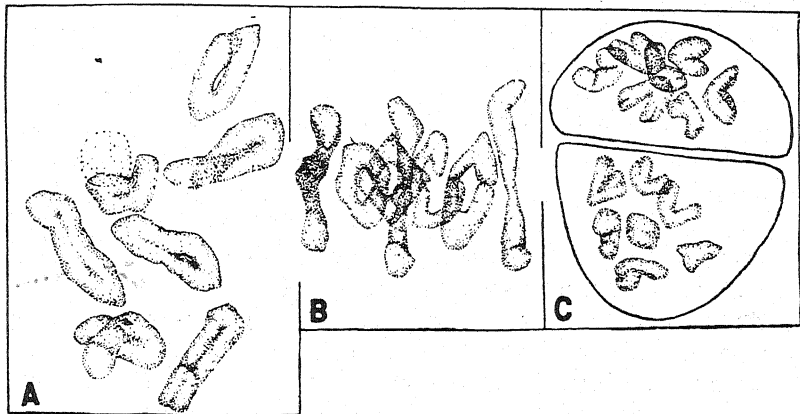


FIG. 67. Chromosomes in *Secale* species.

- A, Diakinesis in *S. cereale* L.; B, heterotypic metaphase in *S. cereale* L.; showing the character, position and shape of the chromosomes at this phase; C, homotypic metaphase in *S. cereale*. (After Longley and Sando.)

On the other hand, Levitzky (1931) in a study of the rye karyotype found no differences of systematic importance. He also concluded that the 8-chromosome plants contained an extra chromosome, and that the formula for such plants should read  $(7 + X) = 8$ . Hasegawa (1934) re-investigated the 8-chromosome forms and found that 7 of their chromosomes corresponded to the 7 chromosomes of the normal type. The eighth chromosome appeared to be an additional form. He therefore agrees with Levitzky that the position is  $(7 + X) = 8$ .

In a detailed study of the cytology of *S. cereale*, *S. montanum* and *S. fragile* (one plant of *S. africanum* was also examined), Emme (1928) found races with 7 and 8 chromosomes in all three species. Measurement of the chromosomes indicated that the length of the chromosomes of "brittle" varieties was much greater than "non-brittle," and that the length of "semi-brittle" was intermediate. He consequently put forward the suggestion that the factors for "brittleness" were situated in the extra chromosomes.

The reduction division was similar in all species but irregularities were frequent. Gametes, with 7, 8 or 9 chromosomes were formed, but as races with 7 or 8 chromosomes only exist, either the gametes or zygotes with the other numbers must be non-viable. This may be in whole or in part the explanation of the partial sterility found in certain varieties.

Levitzky *et al.* (1932) then studied the cytology of crosses between  $14 \times 16$  plants :

14 $\times$ 16 Cross	Number of individuals obtained with chromosomes varying from 14 to 17.			
	14	15	16	17
Exp. 1	1	1	13	—
Exp. 2	1	1	16	1
Reciprocal Exp. 1	1	—	—	—
Reciprocal Exp. 2	3	—	10	—

Irregularities were frequent. The results in general indicate that the majority of the gametes must have possessed 9 chromosomes.

Crosses of 16-chromosome plants *inter se* gave :—4 plants with 16 chromosomes ; 1 with 17 + a fragment ; 10 with 18. All chromosomes above 14 were headed. The selfed offspring of the 18-chromosome plants resulted in 1 plant with 14 chromosomes ; 1 with 16 ; 4 with 18 and 2 with 20.

A free pollinated 16-chromosome plant when studied gave :—2 plants with 14 chromosomes ; 6 with 16 ; 5 with 18.

A 14-chromosome plant grown alongside of a 16, gave rise to offspring, of which 5 had 14 chromosomes ; 6 had 16 ; 1 had 18 and 1 had 25.

It would, therefore, seem that pollination by pollen with the same chromosome number occurred as frequently as with pollen with different chromosome numbers, and that both pollens were equally successful. The 25-chromosome plant must have arisen from the fertilization of a diploid egg of a 14-chromosome plant with a 7 + 4 gamete from an 18-chromosome plant.

Plants with increased chromosome numbers may be fertile ; in the majority of cases they show a reduction in fertility.

Gotoh (1924) and Longley and Sando (1930) have described and figured the

chromosomes. Melburn (1929) and later Gurney (1931) have described in detail the formation of the bivalents in the pollen mother-cells.

Darlington (1933) studied the chiasmata in a paternal type derived from the cross of a "seven" by an "eight." It possessed 7 major chromosomes and a fragment "K." At meiosis the 7 major bivalents showed regular pairing with 1 to 4 chiasmata. (Average per bivalent 2.42.) The *K* fragments often failed to pair. Their chiasma frequency and that of their long and short arms was approximately proportional to their length (0.83; 0.75; 0.08 respectively). (See Fig. 68.)

GERMINATION AND SEEDLING.—Germination may begin within from 36 to 48 hours. The minimum temperature is reported to be between 33 to 35.6 F., the optimum being 77 F., and the maximum at 87 F.

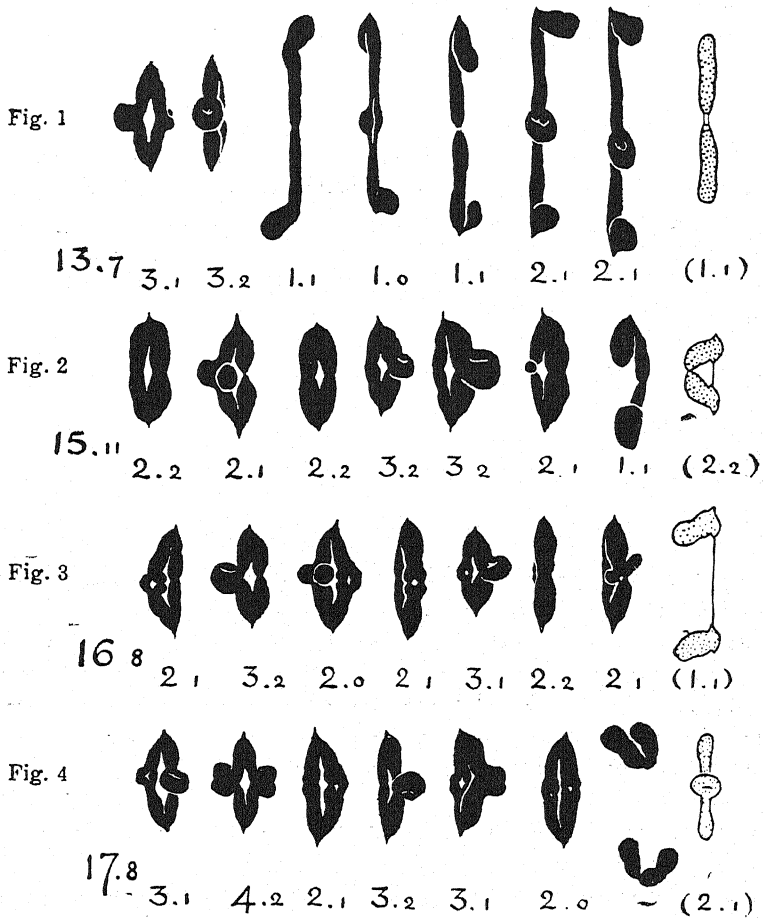


FIG. 68.

1—4. Side views of first metaphase bivalents in *Secale*. Seven major bivalents black, fragment "k" pair stippled. Two major chromosomes unpaired in Fig. 4. (The total number of chiasmata and the number terminal are given in smaller figures under each bivalent. The totals for each nucleus are given at the left.) Notice the different forms assumed by the fragment pair according to the number and position of its chiasmata. X 1600. (After Darlington.)

The primary seminal root appears first, followed by the three secondary seminals. Almost simultaneously the plumule emerges. By elongation of the "mesocotyl," the coleoptile is raised to near the ground level. The adventitious roots develop from the nodes above ground level, but if the grain is deeply planted the first of these roots may form well below ground level.

The coleoptile is closed, and purplish in colour and the first leaf is rolled and also tinged with purple.

**RYE HYBRIDS.**—a. WITH *S. montanum*.—This species differs from cultivated rye in several characters, more particularly in its perennial habit; its fragile rachis and its narrower, smaller grain. Tschermak (1913) found that it crossed readily with *cereale*. Longley and Sando (1930) studied the cytology of the F<sub>1</sub> hybrid. Both parents have the haploid chromosome number of 7 (Stolze, 1925). In the pollen mother-cells of the hybrid there are 7 bivalents, but abnormal behaviour was observed occasionally.

Kostoff (1931-1932) found that the F<sub>1</sub> plants of this cross had about 75 per cent. of abortive pollen. This abortive pollen was apparently due to a retardation of the nuclear division in the pollen at the time of the opening of the anther.

Rye has also been crossed with *S. anatolicum* (Tschermak, 1913; Ossent, 1930).

b. WITH WHEAT.—In these crosses, there is the possibility of producing hybrids with either 14, 21 or 28 chromosomes, depending on the wheat species employed.

1. *Diploids*.—According to Thompson (1926), Einkorn wheat ( $n = 7$ ) cannot be crossed with rye ( $n = 7$ ), but Tschermak states that he obtained sterile hybrids out of the cross *T. monococcum* × *S. cereale*.

Oehler (1931) also failed to obtain hybrids in crossing rye with *T. monococcum* and *T. aegilopoides*.

2. *Triploids*.—Tschermak succeeded in the cross *T. polonicum* × *S. cereale*, and Jesenko (1913) apparently crossed *T. dicoccoides* and *T. dicoccum* with rye.

Zhegalov (1925) obtained one plant which was completely sterile, and rye-like only in the possession of anthocyanin at the base of the shoot, from the cross of *T. durum* var. *melanopus* with spring rye. Plotnikova (1931) also obtained sterile hybrids from the above cross, and also from *T. persicum* v. *fuliginosum*. Oehler (1931) was successful with a rye × *T. durum* cross, but failed with *T. polonicum* and *T. dicoccum*.

Aase (1930) discusses the triploid hybrid *T. durum* (14) × *S. cereale* (7), and Longley and Sando (1930) the triploid obtained by crossing *T. dicoccoides* (14) × *S. montanum* (7). In the first case 0 to 4 bivalents may occur, and in the second no bivalents were found. Florell (1931) obtained no seed in crossing emmer and rye; 2.1 per cent. of florets set seed in the cross Peliss × Rosen and Peliss × Dakold; 0 per cent. in Polish × Rosen and 2.8 per cent. in Polish × Dakold; 2.8 per cent. in Clackamas (Durum) × Rosen and 11.1 per cent. in Clackamas (Durum) × Dakold.

3. *Tetraploids*.—The first tetraploid hybrid produced artificially was obtained by Wilson in 1875. Since then, such hybrids have been obtained in great numbers. The ease with which the cross can be made depends upon the varieties employed and the species used as the seed parent. Thus Jesenko failed

to secure a single fertile grain after pollinating 3,500 rye flowers with wheat pollen ; the reverse cross gave about 6 grains per 1,000 pollinations. On the other hand, Backhouse, using a Chinese wheat, *T. vulgare* v. *albidum*, as parent, obtained up to 80 per cent. of hybrid grain. Thompson (1926) used the same wheat and pollinated it with pollen from the spring variety of rye known as Prolific. He had no difficulty in securing up to 90 per cent. of fertilizations. Leighty and Sando (1928) were equally successful. At the Saratov Experiment Station, Russia, marked differences have been found in the behaviour of wheat varieties. Certain wheats have now been selected that set seed so readily with rye pollen that the mass production of wheat and rye hybrids in the field now presents no difficulties. (Meister and Meister, 1924 ; Meister, N., 1926 ; Meister, N. and Tjumjakov, 1928.) Firbas (1920) in a study of the conditions most favourable to the production of wheat-rye hybrids found that the all-important factor was the variety, and that external conditions, age of pollen and time of pollination had but little effect.

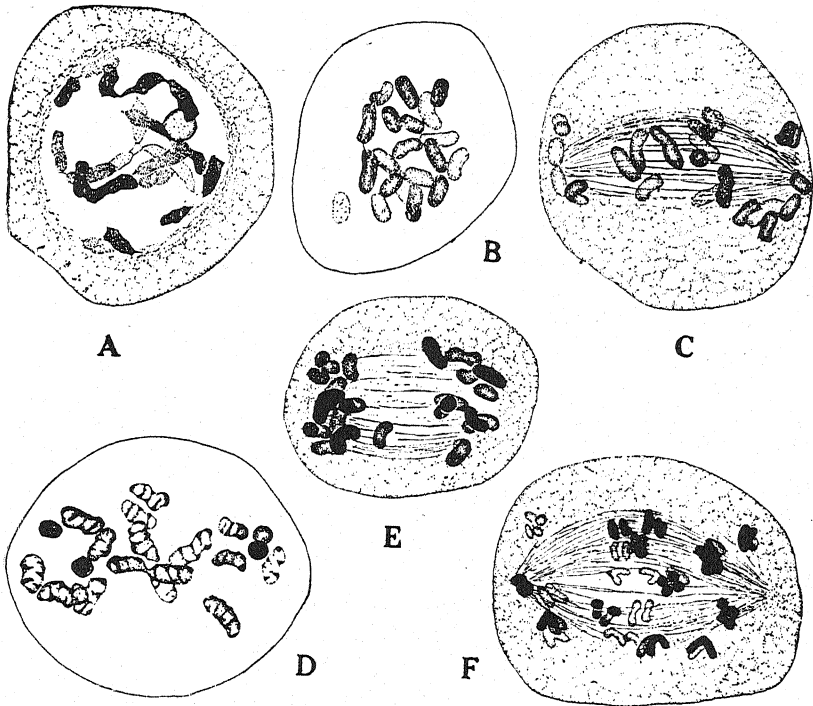


FIG. 69.

Wheat-rye triploid, first meiotic division. *Triticum durum* (14) × *Secale cereale* (7). A, late prophase, some univalent chromosomes attached end to end. B, early metaphase, 21 univalents. C, metaphase, typical distribution of univalents through the entire spindle. D, metaphase, 1 open bivalent and 19 univalents. Differential staining sometimes observed (iron-aceto-carmin). E, anaphase, 10 univalents approaching one pole and 11 the other pole. F, anaphase. Splitting of the univalents occurs before migration to the poles. Univalents lying at the region of the normal equatorial plate will divide. X 1300. (After Aase.)



TABLE XXVIII.

PAIRING OF CHROMOSOMES IN WHEAT-RYE HYBRIDS.

Cross.		Number of Bivalents.	Authors.	Year.
Ovule parent.	Pollen parent.			
<i>T. vulgare</i> .	<i>S. cereale</i> .	0—3	Kihara.	1924.
<i>T. vulgare</i> .	<i>S. cereale</i> .	0—2	Zalensky and Doroshenko.	1924-25.
<i>T. vulgare</i> .	<i>S. cereale</i> .	—	Nikolaewa.	1924.
<i>T. vulgare</i> v. <i>albidum</i> .	<i>S. cereale</i> (Prolific).	0—3	Thompson.	1926.
<i>T. vulgare</i> .	<i>S. cereale</i> .	0—3	Bleier.	1928.
<i>T. vulgare</i> .	<i>S. cereale</i> .	0—4	Bleier.	1931.
<i>T. vulgare</i> (Triplet).	<i>S. cereale</i> (Rosen).	0—3	Aase.	1930.
<i>T. vulgare</i> (Alstrom).	<i>S. cereale</i> (Rosen).	0—4	Aase.	1930.
<i>T. vulgare</i> .	<i>S. cereale</i> .	—	Longley and Sando.	1930.
<i>T. vulgare</i> .	<i>S. montanum</i> .	0—1	Longley and Sando.	1930.
<i>T. spelta</i> .	<i>S. montanum</i> .	0—3	Longley and Sando.	1930.
<i>T. vulgare</i> .				
<i>T. compactum</i> (Hybrid 128).	<i>S. cereale</i> .	0—3	Florell.	1931.

More difficulty has been encountered in producing the hybrids when rye is used as the seed parent. The earlier investigators consistently failed to obtain such a cross. In 1922, however, Gaines and Stevenson obtained the cross and further stated that the *F*<sub>1</sub> and *F*<sub>2</sub> progeny were predominantly rye-like. In 1927, Nina Meister and Tjumjakov, employing "Jelissejer" rye as the ovule parent and *T. vulgare* v. *erythrospermum* No. 648 as the pollen parent obtained 2.46 per cent. of successful fertilizations.

All investigators agree that the *F*<sub>1</sub> hybrids are more or less intermediate with a tendency towards the predominance of either wheat or rye characters. Meister

and Tjumjakov (1928) have compared the hybrids of the direct cross (wheat  $\times$  rye) and the reciprocal cross (rye  $\times$  wheat) of the same varieties. They state that "no matter whether the pistillate parent be wheat or rye . . .  $F_1$  hybrids are perfectly identical in development and fertility, as well as in their morphological characters." This statement is in sharp conflict with the claim made by Gaines and Stevenson (l.c.) that the  $F_1$  and  $F_2$  of their rye  $\text{♀} \times$  wheat  $\text{♂}$  cross showed maternal inheritance with the fertility of the ears varying from 50 to 90 per cent. Buchinger (1931) has confirmed Meister's conclusions.

As regards the fertility, Carman, Rimpau, Miczynski, and Love and Craig claim to have obtained  $F_2$  plants from the self-pollination of  $F_1$  plants. All other investigators have found the hybrids, with certain exceptions, to be completely infertile with their own pollen. Subsequent generations have only been secured by the use of wheat or rye pollen and even then with difficulty. Thus, Jesenko obtained only 1 grain for approximately 5,000 pollinations of  $F_1$  florets with rye pollen; with wheat pollen the rate was 3 per 1,000 pollinations; similar results but with variable rates have been obtained by others.

The  $F_2$  plants obtained by back-crossing with wheat (or rye) are variable but tend to be more wheat-like in appearance. Some are slightly fertile. Continued back-crossing gives rise to still more wheat-like plants. Those which most resemble wheat are the most fertile.

The evidence that more or less constant wheat-rye hybrids can be obtained is now convincing. Rimpau's hybrids (1891) were claimed to have remained constant for 23 generations. Some of Jesenko's hybrids were constant in  $F_4$ . The later work of Tschermak and of Meister (l.c.), Meister and Tjumjakov (l.c.), and Florell (l.c.) amply corroborates.

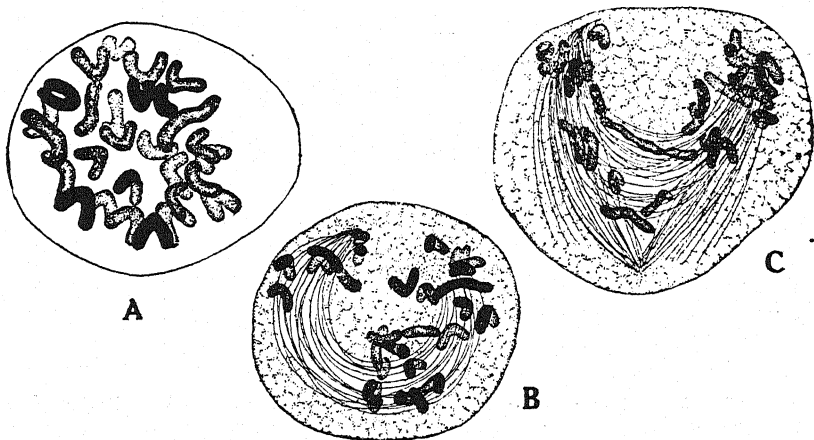


FIG. 70.

Wheat-rye tetraploid, first meiotic division. *Triticum vulgare* (21)  $\times$  *Secale cereale* (7). A, metaphase, polar view, the rarely observed equatorial plate formation of the 28 univalents. The 7 larger chromosomes are probably from rye. B, same stage as in A, but the typical arrangement of the 28 chromosomes over the spindle. Curved spindles are frequently observed. C, combined curved and tripolar spindle. One bivalent is in evidence.  $\times 1300$ . (After Aase.)

Tschermak's constant strains are not only hardy but have given satisfactory gluten and baking tests. Meister's analysis (1927) and those of Kharitanov (1930) and Varsiljev (1932) indicate that, in spite of variation, strains of wheat rye may be obtained which are winter hardy, drought resistant and yet give satisfactory yields and flours of good baking capacity.

Meister (1927 and 1930) has further shown that the segregates obtained from crosses between rye and various Indo-European awned wheats can be divided into coarse Asiatic types and Indo-European types.

Most of the characters usually associated with soft wheats are to be found. This is so striking that Meister has suggested that the bread wheats may have arisen from crosses between Emmer wheats and rye.

The wheat-rye hybrids have been studied cytologically in considerable detail. Table XXVIII indicates the position found in the  $F_1$  generation.

The table clearly indicates that there is marked incompatibility between the chromosomes, and the occasional bivalents produced are united telosyndetically.

The distribution of the bivalents in the  $F_1$  of the cross 128 wheat  $\times$  Rosen rye was found by Florell to be as follows:—

Bivalents per cell.						Cells.	
Number.						Number.	Per cent.
0.	..	..	..	..	..	17	18.3
1.	..	..	..	..	..	25	26.9
2.	..	..	..	..	..	48	51.6
3.	..	..	..	..	..	3	3.2
Total ..						93	100.0

No equatorial plate forms. The univalents are scattered irregularly and segregate apparently at random, with frequent and irregular laggards. Bivalents when present behave normally.

The second or homeotypic division is on the whole more regular, and the equatorial plate more obvious. The number of chromosomes is very variable, but all divide. The resulting tetrads usually have 4 to 8 cells, and are very abnormal. Degeneration follows immediately. At maturity practically all are shrunken and empty. (Thompson, 1926; Florell, 1931.) The prophases in the division (*T. vulgare* v. *albidum*  $\times$  *S. cereale* v. *Prolific*) have been studied by Melburn (1929).

Florell has investigated cytologically the plants produced by back-crossing hybrid 128 wheat  $\times$  Rosen rye with the wheat parent. This hybrid had 28 chromosomes, and must have formed a small number of viable gametes. Ten first back-cross first-generation plants—( $WR_1WR_1$ )—had 40 to 49 chromosomes. As only 21-chromosome pollen was used the gametic chromosome numbers of the  $F_1$  ovules must accordingly have ranged from 19 to 28. Florell considers that those with high chromosome numbers (26 and 28) must have been formed as

somatic gametes ; those with low numbers (19 to 21 or 22) probably by random assortment.

The back-crossed plants with high number, presumably the product of somatic gametes, were more wheat-like and more fertile than those with low chromosome-numbers resulting from gametes produced by random assortment.

The somatic chromosome count of 25 first back-cross third-generation plants ( $WR_1 W_3$ ) and second back-cross third-generation plants ( $WR_1 W_1 W_3$ ) varied from 42 to 47.

A second back-cross third-generation family, segregating only for kernel colour, had 42, 43 and 44 chromosomes. The red-grained plants had 43 and 44 chromosomes ; the white plants 42. Twenty-two bivalents were found in two 44-chromosome red-grained plants ; 21 bivalents in the 42-chromosome white-grained plants. Two families with " hairy neck ", one segregating for grain colour and the other for grain length, had somatic chromosome numbers varying from 43 to 45 and 42 to 47 respectively. All the plants had 1 to 5 univalents except one plant which had 22 bivalents. Pollen formation was abnormal in all.

Recently Bleier (1933) has studied the wheat-like segregates with 42 chromosomes obtained at Saratov with rye and *T. monococcum*, *T. durum* and *T. vulgare*. Those with *T. vulgare* were successful in 33 per cent. of cases ; with *durum*, 29 per cent. ; with rye 3 per cent. ; with *T. monococcum* 0 per cent.

The hybrids obtained from back-crossing with rye were typical wheat-rye hybrids, and were completely sterile. Those with *T. durum* were slightly fertile ; those with *vulgare* fully fertile.

In the fertile offspring, the majority had 21 bivalents, although 31 per cent. of the cells had 1 to 2 univalents present. No lagging of chromosomes was noted, but 15 per cent. of the pollen was functionless and contained one chromosome short or one in excess.

In the hybrids with *T. durum*, 79.5 per cent. of the metaphase figures had  $14'' + 7'$ . The whole behaviour paralleled that of a normal *T. durum*  $\times$  *T. vulgare* cross.

In the  $F_1$  hybrid with rye, three-quarters of the cells contained 28 univalents.

Bleier comes to the conclusion that the behaviour of these crosses indicates that all trace of the rye chromosomes has gradually disappeared, and that the differences noted in these so-called wheat-rye hybrids and the original wheat parents, must be due to out-crossing with rye. Consequently, any value of wheat-rye crosses would lie in the possibility of obtaining fertile amphidiploids.

He also points out that the complete absence of gemini in the back-crosses with rye would seem to indicate little or no homology with wheat.

Although wheat-rye hybrids were at first stated to be infertile, this is by no means absolute. Thus, Tjumjakov (1927, 1930) obtained 149, 116 grains from 18,150 hybrids during the period 1918-25. From each line of wheat used in the parentage, hybrid strains of varying fertility were obtained. Though the fertility of each strain was approximately constant, climatic conditions influenced the fertility mean of all. One plant, indeed, produced as many as 35 grains ; normally, however, the fertility was low, and only about 5 per cent. of the seeds sown produced  $F_2$  plants. They exhibited segregation into a series of forms ranging from wheat-like to rye-like plants. Of the intermediate types, 43.4 per cent.

were completely sterile ; the remainder were slightly fertile and usually segregated in the  $F_3$  generation into wheat-like and intermediate forms. Later a few  $F_1$  intermediates were found, which exhibited marked fertility. (Tjumjakov, 1928 and 1930 ; Meister, 1930.) In subsequent generations, no segregation of the  $F_1$  characters occurred, and the fertility was maintained, though the percentage of "good pollen" was lower in the  $F_2$  generation than in the  $F_1$ , and in the subsequent generations.

Cytological examination of these constant hybrids indicated that they possessed 56 chromosomes, the sum of the diploid chromosome numbers of the parent wheat ( $2n = 42$ ) plus those of the rye parent ( $2n = 14$ ). In these hybrids, accordingly, duplication of the whole complement of 28 chromosomes received from the parents (21 from wheat + 7 from rye), must have taken place.

The situation is therefore analogous to that of the constant *Brassica-Raphanus* hybrids, *Aegilotriticum* and others.

Similar constant hybrids have been obtained by Lewitsky and Benetzkaia (1930), who later (1931) published a detailed cytological study of their behaviour.

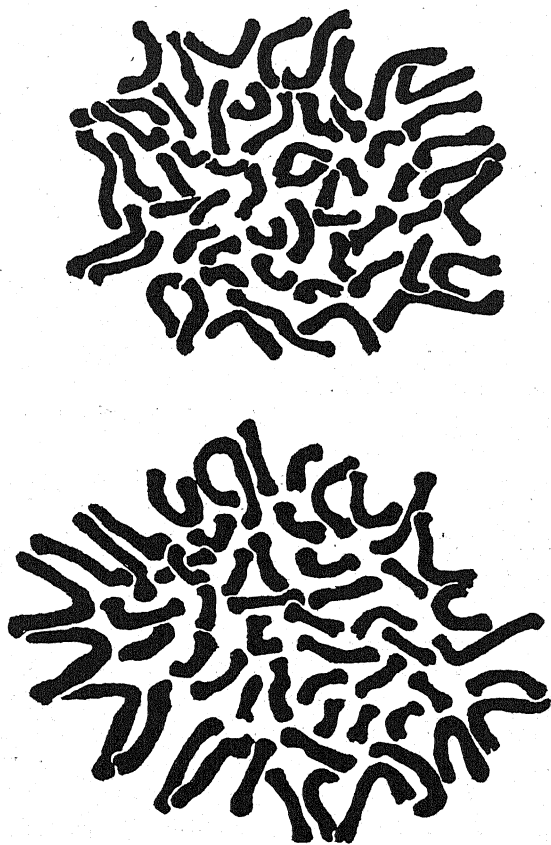


FIG. 71.

Camera-lucida drawings showing two somatic metaphase plates of  $F_5$  Purplestraw wheat  $\times$  Abruzzes rye amphidiploid. ( $2n = 56$ ).  $\times$  about 1,375. (After Florell.)

All (as noted above) had 56 chromosomes. Irregularities were observed at meiosis, the most characteristic being the presence of lagging chromosomes and univalents. In spite of such irregularities the progeny retained a complement of 56 chromosomes. There must, therefore, be a selective action.

No satisfactory evidence as to the origin of these auto-tetraploids was obtained. The few ovules examined showed 28 chromosomes after diakinesis. Since no viable pollen was present, there must have been an increase in the chromosome numbers in the ovules.

The grain of the constant hybrid is said to be rye-like in shape, but wheat-like in colour and embryo. It appears to be more cold resistant than either parent, and strains have been obtained which are high yielding and early ripening. Baking tests also indicate that the flour of certain strains may produce satisfactory bread. (Kharitanov, 1930.)

From the above it would appear that approximately constant wheat-rye hybrids with low chromosome numbers and definitely constant hybrids with high chromosome numbers, can be obtained.

c. WITH AEGILOPS.—Tschermak in 1913 obtained *Aegilops*—Rye hybrids. Similar hybrids were secured by Leighty, Sando and Taylor (1926) with *A. ovata* and *A. triuncialis*; and by Karpechenko and Sorokina (1929) with *A. triuncialis*. All the plants were completely sterile. Later, Leighty and Sando (1927) secured hybrids with *A. ventricosa*  $\times$  *T. turgidum* with rye. The two plants obtained were absolutely sterile, but exhibited characters of all three genera.

Berg (1931) studied the triploid hybrid *A. triuncialis*  $\times$  *S. cereale*. There were 5 to 7 bivalents with 11·7 univalents. Thompson (1931) has accordingly suggested that the rye chromosomes are homologous with the D. set of *triuncialis*, and so have no homologies with those of wheat.

Although all the above *Aegilops*-Rye hybrids were sterile, Bleier (1931) obtained three plants out of the cross *A. ovata*  $\times$  Rye. They were identical in appearance, exhibiting many rye characters and some *Aegilops* characters. The fertility was relatively high, and 104 grains germinated. The F<sub>2</sub> plants were less fertile than the F<sub>1</sub>, but otherwise were very similar. Segregation, however, occurred in the F<sub>3</sub> generation.

CLASSIFICATION AND ORIGIN.—There is but one species of cultivated rye, *Secale cereale* L. It is closely related to the wild species, *S. montanum* which, as noted above, has the same chromosome number ( $n = 7$ ) and is readily crossed therewith. Many botanists, accordingly, have accepted the hypothesis that *S. montanum* is the progenitor.

Tschermak (1914) and Schultz (1919), however, believe that the prototype of the cultivated rye is *S. anatolicum* Boissier, a species indigenous to Syria, Persia, Afghanistan and Turkestan. Other wild species, however, are known. Thus, in addition to *S. montanum*—essentially a western form, though spreading eastwards—there are now known to be at least three eastern species, *S. anatolicum*, *S. ciliatoglume* (Boiss) Grossh., and *S. Vavilovii*, Grossh. All are closely related to *S. cereale*, but *S. Vavilovii* appears to be intermediate between *S. montanum* and *S. cereale* (Grossheim). On the other hand, Vavilov (1917) found *S. cereale* widely distributed throughout South-Western Asia in fields of barley and wheat in districts where rye is not grown as a cultivated crop.

It would therefore appear that *S. cereale* is a "secondary crop," and that the weed forms are transitional to the cultivated.

Zhukovski has accordingly extended the concept of the species *S. cereale* and subdivided it as follows :—

- a. Sub-species *cereale* Zhuk.  
Mature spikelets with the rachis tenacious ; in cultivation.
- b. Sub-species *ancestrale* Zhuk.  
Mature spikelets completely fragile ; (? semi-cultivated).
  1. var. *Afghanicum*, Afghanistan.
  2. var. *Spontaneum*, Zhuk.  
A biennial form found in Lydia and Asia Minor.
- c. Sub-species *segetale*, Zhuk.  
Mature spikelets fragile but breaking at two-thirds to one-third of the spikelet : segetal.
  1. var. *articulatum*, Vav.
  2. var. *asiaticum*, Vav.
  3. var. *Sub-articulatum*, Vav.

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## CHAPTER VI

### BARLEY

BARLEY is an annual cereal generally treated as a summer crop but in sub-tropical countries as a winter one. Winter-hardy forms, however, are known, generally associated with a so-called "winter-habit" of growth.

**ROOTS.—1. SEMINAL ROOTS.**—The total possible number of seminal roots (mostly preformed in the embryo) is eight. Many plants may possess fewer than eight. Of these roots, one or more tend to grow vertically downwards and, maintaining their lead, may penetrate to a depth of 5 to 6 feet. They are branched throughout their length. The remaining roots tend to spread out horizontally, or slope downwards at a slight angle. They ultimately reach a length of some 2 to 16 inches, and a depth which varies from 2 to 12 inches. They also are branched throughout.

**2. ADVENTITIOUS ROOTS.**—The true adventitious roots spring from the nodes near ground level. They are first noticed just before tillering commences. Many of these roots are at first short, unbranched and comparatively thick. They are white in colour and carry root hairs throughout their length. Later, they elongate, lose their white glistening colour and become branched throughout. A few of the adventitious roots penetrate deeply, reaching a depth of some 4 to 5 feet, at times exceeding the depth reached by the vertical growing seminal roots. The remainder either spread horizontally or grow downwards at an angle. They fill the upper layers of soil with a dense mass of rootlets. On the whole, the habit is very similar to that of spring wheat and oats, but the fineness of the roots, their degree of branching and lateral spread are more or less intermediate. Differentiation into a shallow growing upper region and a more deeply penetrating lower region is often marked (Weaver, 1926).

Soil conditions and fertilizers markedly influence the development. In heavy soils and under drought conditions, the roots may be very shallow and widely spreading. The use of artificial fertilizers, whether containing potassium, nitrogen or phosphorus, tends to increase the root system to a marked extent. Sodium nitrate, with or without superphosphate, gave the greatest effect. (Brenchley, 1921.)

The so-called "white roots" constitute the first stage in the development of many of the secondary roots. Roots of this type are generally found up to the time when the growth of the shoots begins to predominate over the growth of the roots (a period of 10 to 12 weeks). Thereafter they lose their special characteristics and assume the characters of the other roots of the system (Brenchley, 1921). As we shall see later, white roots differ from the others in their anatomy (Jackson, 1922).

**ANATOMY OF THE ROOT.—1. SEMINAL ROOTS.—a. The young stage.**—Within the piliferous layer, 4 to 6 layers of large, somewhat irregularly shaped

cortical cells, occur. This is bounded by the endodermis, a single layer of tangentially elongated cells, their walls in the young stage unthickened. The stele, of moderate dimensions, is bounded by a pericycle whose cells are elongated radially and are continuous, except opposite the 6 to 7 xylem groups where protoxylem elements abut directly on the endodermis. Each xylem group consists, in addition to the protoxylem, of a single large vessel. The phloem alternates with the xylem, its cells not readily distinguishable from the rest of the thin-walled ground tissue. The centre of the stele is occupied by what appears to be a duct bounded by thin-walled cells. It is, however, of the nature of a vessel and in the end differentiates

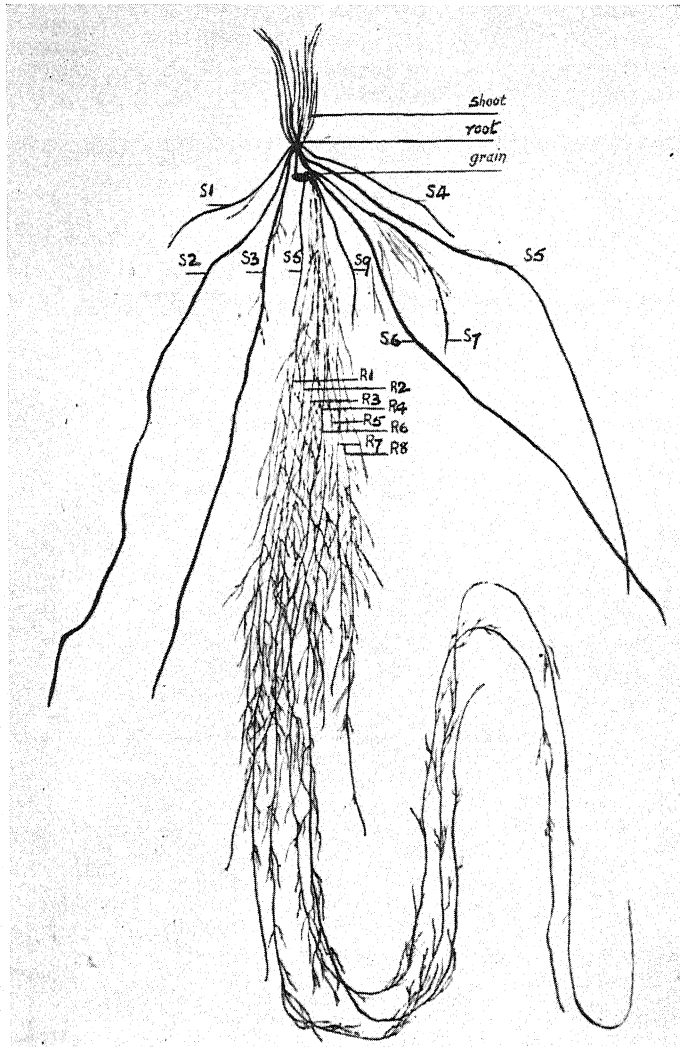


FIG. 72. Root System of Barley, with branched and unbranched roots.  
 R1 to R8, branched roots.  
 S1 to S9, unbranched roots. (After Jackson.)

as such. In origin, it is similar to the central vessel found in wheat and to the several large primary vessels found in maize.

b. *The intermediate stage.*—The endodermis is definitely thickened along its inner and, to a less extent, its radial walls. The elements of the pericycle also are thickened throughout.

c. *The mature stage.*—In the mature roots, the whole of the stele has undergone marked thickening. This is most obvious in the cells of the

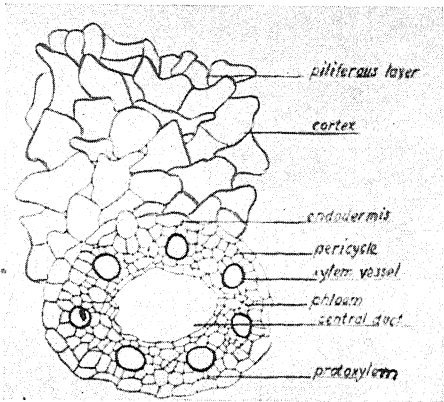


FIG. 73. T.S. of young branched root. (After Jackson.)

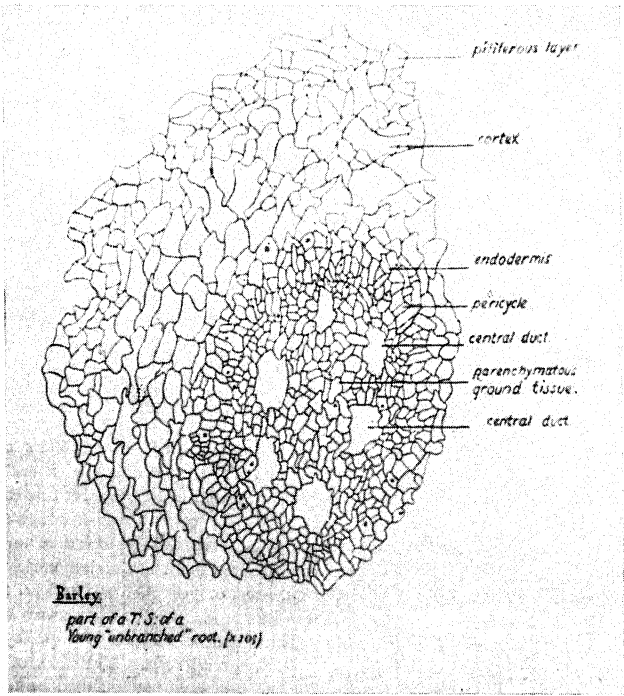


FIG. 74. Part of transverse section of young unbranched root. (After Jackson.)

endodermis; somewhat less obvious in the cells of the ground tissue and the pericycle. The central duct is now an unmistakable vessel with scalariform thickening. The piliferous layer and some of the cortical tissue may be lost.

2. ADVENTITIOUS ROOTS.—The true adventitious roots show essentially the same structure as do the seminal roots.

3. WHITE ROOTS.—White roots may be seminal or adventitious. The number of seminal white roots is always limited; adventitious white roots may be very numerous. In all cases, a white root is short, comparatively thick, unbranched and carries root hairs throughout the whole of its length. Later, a white root may lengthen, develop laterals and in time assume all the characters of the normal roots. (Brenchley, 1921.)

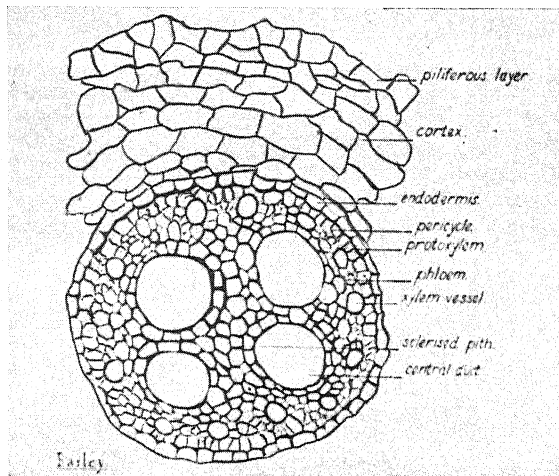


FIG. 75. Transverse section of a "transition" root. (After Jackson.)

a. *The young stage.*—Piliferous layer and cortical layers are as above. The endodermis consists of unthickened tangentially elongated cells. The stele as a whole is thin-walled. Its pericycle is as before. The centre is occupied by a core of parenchymatous cells traversed by 5 to 8 large cells each equivalent to the single large cell (duct) described above. Xylem and phloem are arranged as in the other roots, but at this stage are poorly differentiated.

b. *The intermediate stage.*—The stele is here practically unthickened. There are similar large cells (ducts) traversing the core of parenchymatous cells, and the xylem groups, each with a single large vessel, form a circle outside the ring of the ducts. The phloem is still undifferentiated.

c. *The mature stage.*—The inner and radial walls of the endodermis may be thickened, but not opposite the protoxylem. The cells of the pericycle are uniformly thickened, but they are interrupted opposite the protoxylem groups which abut directly on the endodermis. The central ducts are as before, with the boundary wall still thin. The ground tissue separating these ducts, however, is now thickened. The xylem groups are better differentiated and so is the phloem. The ground tissue between xylem and phloem is unthickened.

The structure as a whole appears to be adapted to the rapid translocation of water and solubles—in particular, the large unthickened central ducts, the general absence of thickened walls, especially in the endodermis, and the presence of root hairs throughout the length. (Jackson, 1922.)

4. TRANSITION ROOTS.—The majority (if not all) of the white roots ultimately elongate, branch and lose their special characteristics. When this happens, the roots at the base show a stele with much more thickened tissue ; an endodermis

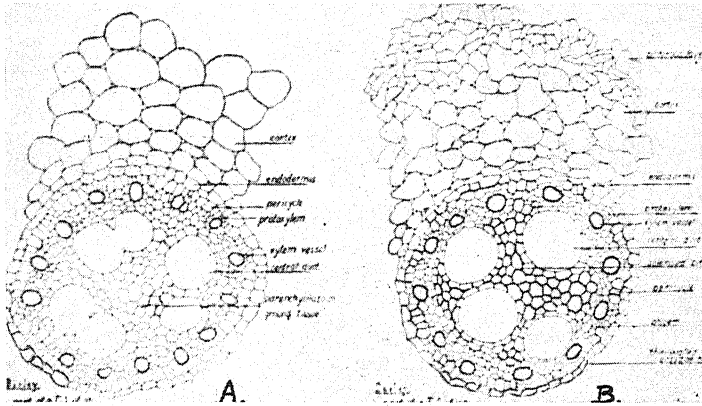


FIG. 76.

- A. Part of transverse section of an intermediate unbranched root.
- B. Part of transverse section of an old unbranched root. (After Jackson.)

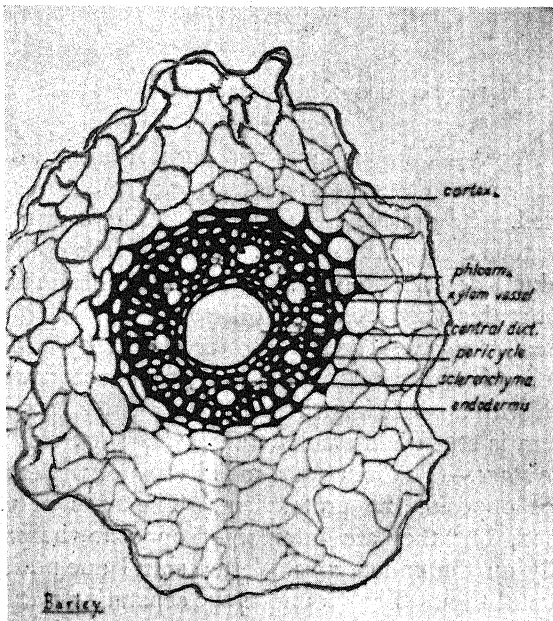


FIG. 77. Transverse section of old branched root. (After Jackson.)

with much thickened inner and radial walls ; ducts whose boundary walls are thickened, and more clearly differentiated phloem. If sections of such elongating transition roots are cut near the apices, it will be found that the new tissue formed is similar to that of the normal root, with but one duct and fewer xylem groups and earlier differentiation of the phloem. (Jackson, 1922.)

STEM.—The stem possesses 5 to 8, sometimes up to 13 nodes ; the inter-nodes elongate from below upwards. The last inter-node carrying the

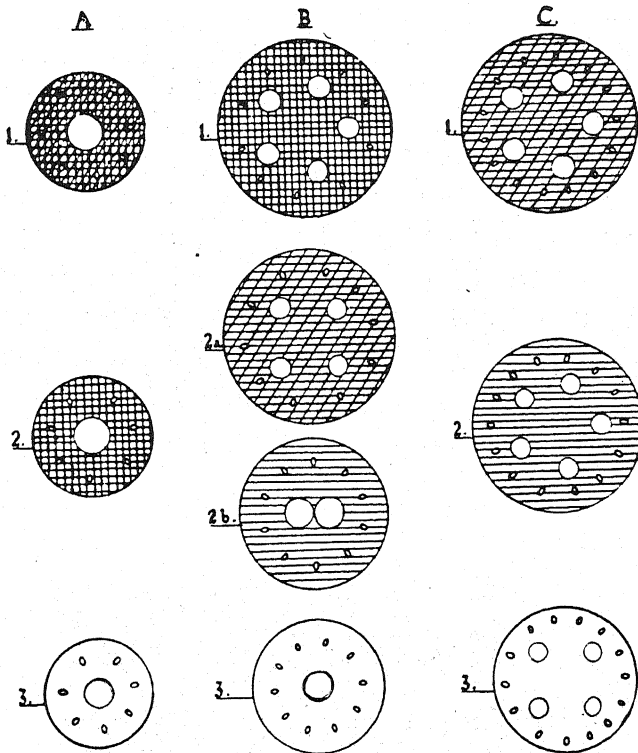


FIG. 78. Diagrams illustrating stellar structure of different root types.

- A. Branched Root. 1, near grain ; 2, middle of root ; 3, behind root tip.  
 B. "Transition" Root. 1, near grain ; 2a, middle of root ; 2b, nearer root tip ; 3, behind root tip.  
 C. "Unbranched" Root. 1, near grain ; 2, middle of root ; 3, behind root tip. The lining indicates the degree of thickening. (After Jackson.)

spike may show considerable variation, and in a few varieties may be so short that the spike is barely exerted. The tillers, though fewer in number than in wheat, develop in the same way. The young plants of early maturing varieties are usually erect, tufted and but little branched ; those of late maturing varieties tend to develop a spreading habit with more numerous short branches. According to von Ubisch (1919), culm length is due to one main factor with two secondary factors. Barbacki (1929) considers that the factors responsible are cumulative. Instances of dwarf types are known ; in one instance it was found to be dominant



to normal (Miyazawa, 1921); in another it behaved as a simple recessive (Harlan and Pope, 1922).

**LEAVES.**—The foliage leaves resemble the leaves of the wheat plant, but exhibit considerable variability in number, colour, length and width. The ligule is well developed and the auricles are more conspicuous than in any other cereal.

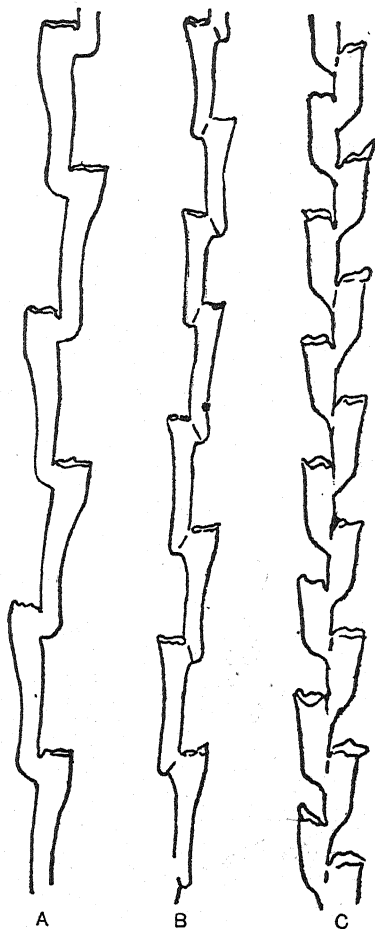


FIG. 79. Relative length of rachis inter-nodes of barley of different densities ( $\times 6$ )  
A, Lax; B, erect; C, very dense. (After Wiggans.)

Leaf size has been studied genetically by Miyazawa (1929). Chlorophyll deficient types have been studied by Nilsson-Ehle (1913, 1922), Hallquist (1924 and 1926), and others. In some cases the amount of the chlorophyll increases with temperature. Recently, Euler and Bergman (1933) have studied the chloroplasts of a number of chlorophyll deficient forms, and have also shown (Euler et al., 1933) that the so-called Albino forms are entirely devoid of chlorophyll, carotin and xanthophyll, whilst a xantha type contained only one-third of the content of normal plants.

Variegated forms have been studied by Sô (1921) and Imai (1928). In these instances the plastids mutate to colourless at certain stages in the development and in certain places. There is here an inherited factor, but the inheritance is also maternal.

**INFLORESCENCE.**—The inflorescence is a cylindrical spike carrying an alternating series of spikelets. The main axis or rachis is strongly compressed and truncated. It consists of a series of straight joints which end in a more or less flat cushion upon which the spikelets are inserted. Each joint is attached to the preceding one at a point directly opposite and extending for a slight distance below the point of insertion of the spikelets. The rachis is tough and does not disarticulate except in a few types where there is a variable tendency to shatter.

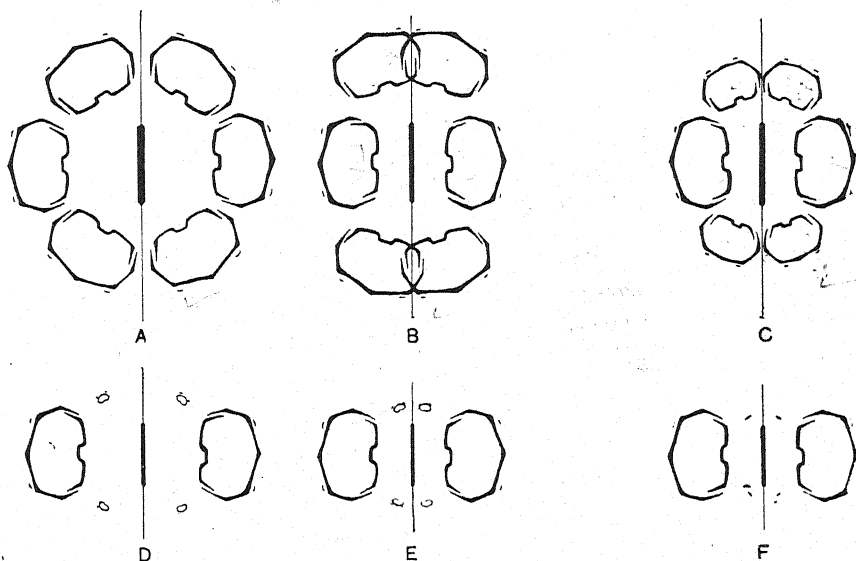


FIG. 80. Diagrammatic sketch of cross-sections of spikes of various types of barley. A, B and C, "Completurn" series: A, Dense form of Aequale Type; B, Lax form of Aequale Type; C, Inaequale Type. D, E and F, "Incompleturn" series: D, Dense form of Semi-deficiens Type; E, Lax form of Semi-deficiens Type; F, Deficiens Type. (After Wiggans.)

The length of the inter-nodes of the rachis is very variable and is the deciding factor in density. (Atterberg, 1899; Harlan, 1914.) In 2-rowed forms, three groups may be distinguished: (1) those with inter-nodes averaging 3.3 cm.; (2) those with inter-nodes averaging 2.5 cm.; and (3) those with inter-nodes averaging 1.7 cm. The 6-rowed types may be similarly divided but the third group (1.7) is not so well defined. In both types, however, varieties which show marked variation occur. The angle of insertion of the spikelets and later of the grain on the rachis depends on the nodal length. The shorter the inter-node the greater is the angle; the longer the inter-node the shorter the angle.

Density has been studied genetically by several investigators. Biffen (1907) found that lax ears were on the whole dominant to dense, but the F<sub>1</sub> was generally intermediate. Von Ubisch (1919) considered there was one main factor with two

subsidiary. Hayes and Harlan (1920) concluded that in some cases density was due to one main factor, in other cases to two or three factors. Vik and Lunden (1928) assumed two factors; Neatby (1929), one main factor with modifying factors; and Huber (1929), two independent factors.

At each joint of the rachis there are 3 spikelets, each one flowered. Each spikelet is borne on a short secondary axis or rachilla, which projects beyond the spikelet and appears as a distinct bristle in the groove of the mature grain.

The development of the 3 spikelets at each node is variable and the following possibilities are known :—

- (1) All 3 spikelets fertile; awned or hooded; developing grains.
- (2) All 3 spikelets fertile; the laterals unawned, their lemmas ending either acutely or obtusely. Grains of laterals about half the size of the median.
- (3) The central spikelet fertile; the laterals infertile, possessing rudimentary vegetative and reproductive organs.
- (4) The central spikelet fertile; the laterals infertile with vegetative parts very much reduced and abortive reproductive organs.

The inheritance of the sterility character is a complicated one. In each of the four groups, sterility has been found by most investigators to be dominant to the more fertile condition, since each group shows progressive sterility. Engledow (1920, 1921) has postulated that they form a series of multiple allelomorphs. Von Ubisch (1916 and 1919) postulated two factors for sterility and Gillis (1926) three: Harlan and Hayes in 1920 obtained the "intermedium" form in the homozygous condition and found that two factors, with indications of a third, were necessary to explain the results. Nevertheless, as Engledow (1924) has shown, the fluctuation of the character is so great that accurate classification of the F<sub>2</sub> segregates is extremely difficult. This position is strengthened by the fact that fertile lateral florets may occur in typical 2-rowed barleys. Thus, Harlan and Martini (1935) state that out of 408 varieties of supposedly normal 2-rowed barleys under observation, 44 produced occasional fertile lateral florets in the 1933 season. They believe that different levels of fertility occur, not only in the flowers but correlated with the vigour of plant growth. It is, indeed, possible to find forms which bridge, by more or less definite steps, the gap between the typical 2-rowed barleys and the fixed *H. intermedium*.

Veideman (1927) is of the opinion that fertility is the physiological result of the anatomical structure and function of the pedicel, and as a consequence not an independent heritable character.

It should also be noted that replication of spikelets may very occasionally occur. When this happens, three series of 3 spikelets instead of one series of 3 spikelets is to be found at each node. In a 2-rowed barley such replication would give rise to an irregular 6-rowed type, the product of 3 fertile with 6 infertile spikelets at each node. In most cases, however, the replication occurs towards the base of a spike and involves only a limited number of nodes.

The rachis at the base of the ear is surrounded by a ridge of tissue which has been termed the "collar"; Arber (1929) interprets this ridge as the much reduced sheathing region of a leaf. Though non-vascular, the fact that it may carry a bud in its axil supports this conclusion.

The spikelets proper are not supported by leaves, but these may be present rarely at the base.

DEVELOPMENT OF THE SPIKELET.—Schuster (1910); Noguchi (1929); Purvis (1934) and Bonnett (1935) have described the development of the ear. Two phases may be distinguished. In the first phase, the stem inter-nodes remain short, the leaves increase in size, and the only structures that differentiate from the growing point are leaf initials. During this stage the growing point above the base remains smooth in outline but increases in length. The beginning

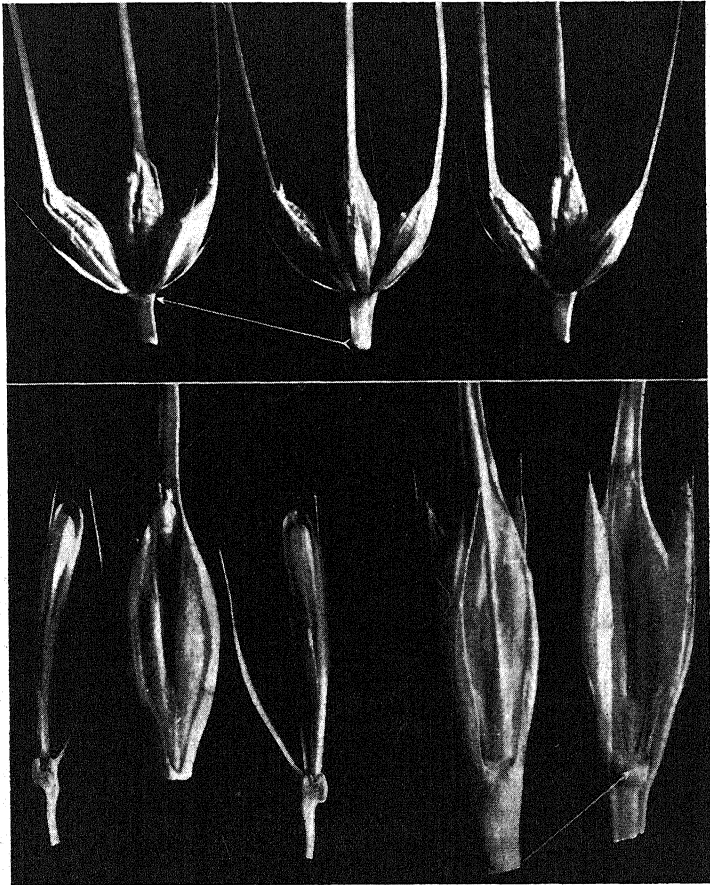


FIG. 81. 6-rowed and 2-rowed barley compared.

Above: Three spikelets of 6-rowed barley showing the development of the 3 kernels which make up the spikelet. These spikelets are built up into heads by superposing them one on the other as is indicated by the white arrow. Below: Enlarged spikelets of 2-rowed barley showing how they are made up of a single developed kernel with the lateral flowers abortive. The remarkable regularity with which the lateral flowers abort in the 2-rowed forms is a striking evidence of the regularity of genetically controlled processes. In some crosses of 6-rowed  $\times$  2-rowed forms varying tendencies for the development of the lateral flowers are noted. (After Harlan, by permission of the Journal of Genetics.)

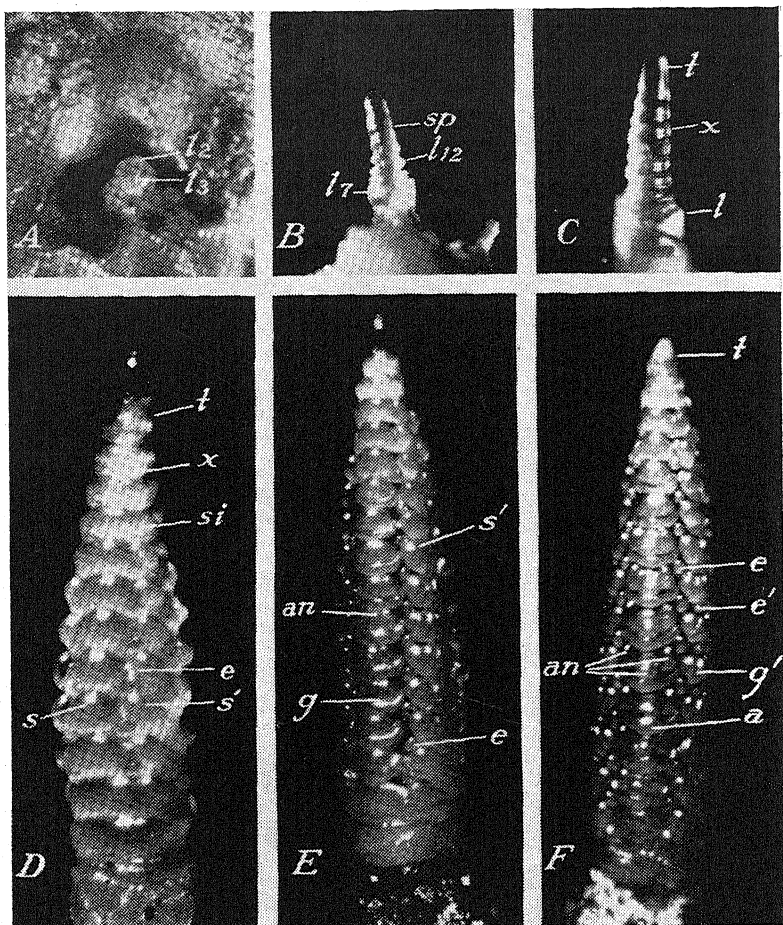


FIG. 82.

- A, A part of the embryo of a kernel of barley with the coleoptile and first leaf removed :  $l_2$ , Second leaf ;  $l_3$ , third leaf. X 21.
- B, Growing point of a barley stem in the 3-leaf stage :  $l_7$ , Seventh-leaf initial ;  $l_{12}$ , twelfth-leaf initial ;  $sp$ , spikelet primordium. X 17.
- C, Growing point of a 6-row barley stem in the 4-leaf stage, showing double ridges marking the beginning of spike differentiation :  $l$ , Leaf initial ;  $x$ , double ridge ;  $t$ , tip of spike. X 25.
- D, Young spike of 6-row barley from a stem in the 5-leaf stage, showing the beginning of spikelet formation :  $s$ , Central spikelet ;  $s'$ , side spikelet ;  $e$ , empty glume ;  $si$ , spikelet initial ;  $x$ , lower of a double ridge ;  $t$ , tip of spike. X 40.
- E, Spike of a 6-row barley stem in the 5-leaf stage when the lemma and anthers begin to form. Stain has been used to make clear the position of the spike structures :  $e$ , Empty glume ;  $g$ , lemma ;  $an$ , anthers ;  $s'$ , side spikelet. X 25.
- F, A spike of 2-row barley from a stem in the 6-leaf stage showing a more advanced stage of glume, anther, and awn development. Stain has been used to mark out the structures :  $a$ , Awn ;  $an$ , anthers ;  $g'$ , lemma of a side spikelet ;  $e'$  and  $e$ , empty glume initials of the side and central spikelets respectively ;  $t$ , tip of spike partially dried. X 25. (After Bonnett.)

of the second phase is marked by the elongation of the inter-nodes of the axis and the formation of double ridges on the growing point. Thereafter, during the second phase, the inter-nodes elongate further and the initials of the spike and spikelets differentiate and develop.

According to Bonnett (l.c.), the sequence of differentiation is as follows:—spikelet initials, empty glumes, lemma, palea, anthers, awn and pistil (Figs. 82 and 83). These two phases are probably related to the fact that in the cereals some vegetative growth must precede the formation of the inflorescence. According to Purvis (1934) no known treatment can induce differentiation of flower initials until a certain minimal number of leaves has been formed. In spring rye, Purvis (l.c.) found this number, under long days, was approximately 7 and the same number may also prove to be correct (approximately) for barley which appears to belong to the same category.

**FERTILE SPIKELET** (of 6- or 2-rowed types).—At the base of the spikelet are 2 long narrow bracts, almost parallel to one another, constituting the glumes. In most varieties they are lanceolate, hairy to glabrous and end in a fine awn-like bristle. Occasionally ovate glumes occur (Beaven, 1902; Harlan, 1918). The awns on the outer glumes may be almost as long as the awns on the lemmas (Munro and Beaven, 1900), whilst Wiggans (1921) noted the very rare occurrence of hoods replacing the awns on the two outermost glumes. The position of the glumes has led to diverse interpretations of their nature (Hochstetter, 1847; Körnicke, 1885; Hackel, 1887; Schuster, 1910). Recently, Arber (1929) made a comparative study of the structure and came to the conclusion that they must be regarded as true glumes, and not halves of a single glume or sterile spikelets, as has been postulated. Behind these glumes the solitary flower is inserted, enclosed in lemma and palea. The lemma is broad, rounded on the back, with 5 nerves—1 dorsal and 4 laterals—which are most obvious towards the apex. In some varieties the lateral nerves are smooth; in others more or less barbed.

In narrow lax-eared barleys, the lemma is attached to the axis by a very narrow band of tissue; on disarticulation, it leaves a smooth surface. This surface is also oblique to the long axis of the grain, and a horse-shoe shaped depression is found just above the line of attachment. (Fig. 84 (a and b).) In dense erect-eared forms, the attachment is broader, and disarticulation then leaves a rougher basal surface. The horse-shoe shaped depression is absent, but when the central nerve is not too large and not continued too far to the base, a transverse furrow is situated above the attachment (Atterberg, 1889). (Fig. 84 (c and d).) These characters may be obvious in hulled grains.

The lemma ends normally in a long awn with strongly barbed, but occasionally smooth edges. Some varieties have deciduous awns but in most the awns are markedly tenacious. Awnless types are also known. In hooded barleys the lemma ends in a 3-lobed structure with the middle lobe hooded. Its nature is very uncertain. Within the hood, one or more accessory spikelets may occur. It has been suggested that the 3 lobes represent a reduplication of the spikelet triplet at the base. Arber (1929) studied the structure comparatively, but came to no definite conclusions—"We can only say that the lemma behaves to the accessory spikelet exactly as if it were that spikelet's parent axis."

Genetically, one to three factors have been postulated, with hoods dominant

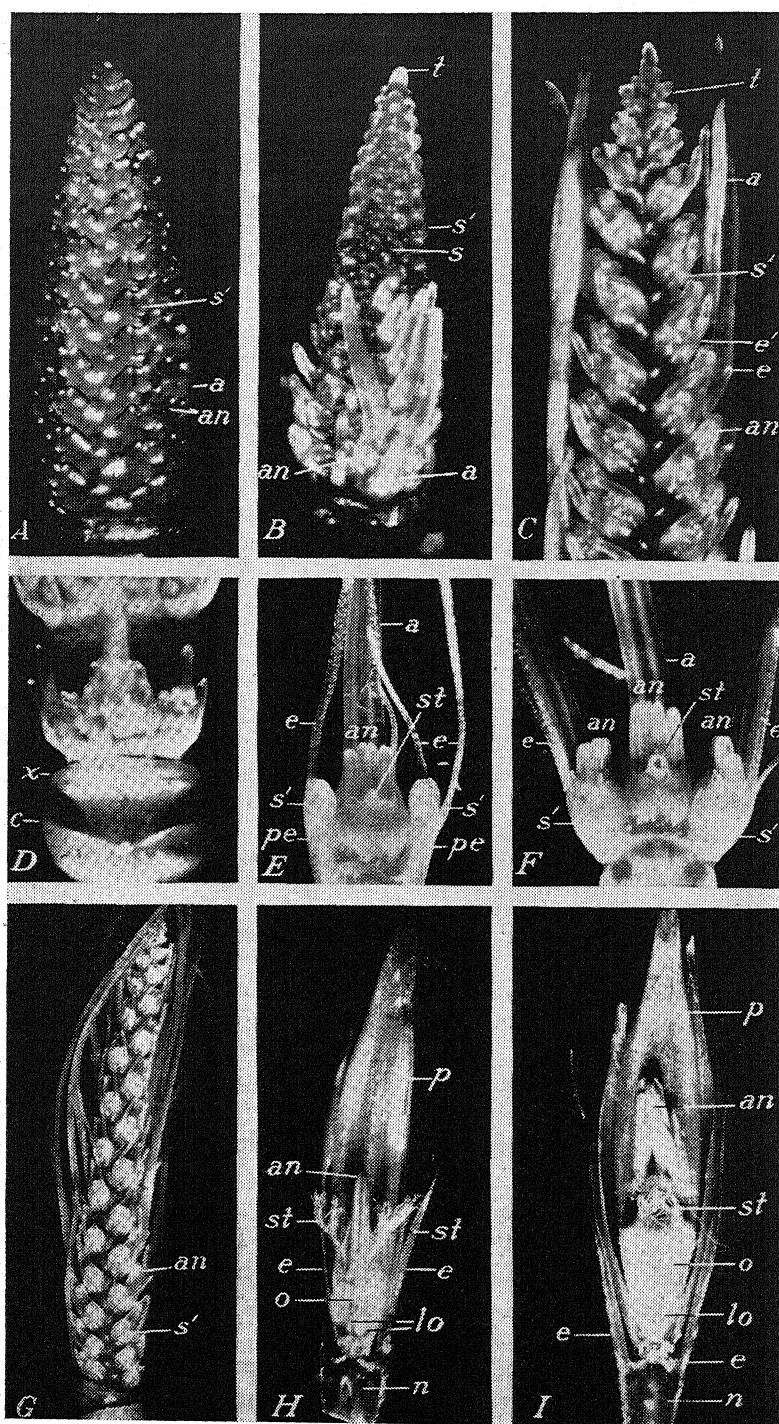


FIG. 83.

(Miyake and Imai, 1922 ; Imai, 1921 ; von Ubisch, 1923). Harlan (1931) has pointed out that the hooded type originally came from Nepal. In a cross between "Everest" and "Manchuria," a sterile hybrid mutant was obtained which was hooded. Neither parent was hooded. Since the "Everest" parent came from Nepal, Harlan suggests that the hooded type may have first arisen there as a mutant.

The innermost bract—the palea—is less obvious, being narrower and largely hidden by the enveloping lemma. It is about the same length as the lemma, is awnless and bears two ridges.

The lodicules are 2 in number, opposite the palea, and generally conspicuous. There are 3 stamens with versatile anthers and slender filaments which are at first short. The ovary is more or less ovate, crowned by 2 feathery stigmas.

INFERTILE, LATERAL OR STAMINATE SPIKELET.—The central spikelets are always fertile on normal ears. The laterals, however, may be infertile. When infertile, two conditions occur :

- (a) With rudimentary reproductive organs. Here the glumes are similar but narrower than on the fertile spikelets. The lemma and palea are also similar though reduced in size, and there is no terminal appendage to the lemma.
- (b) Without reproductive organs. The glumes show further reduction ; lemma and palea are very much reduced ; in some cases a rudimentary rachilla behind the glumes is the only vestige of the flower that survives.

FUNCTION OF THE AWN.—In the great majority of the barleys, the awns are conspicuous and markedly developed. Even at a very early date in development the awns of the fertile flowers are well advanced. Several authors have suggested that they are essentially organs of transpiration. This conception is supported

- A, Spike of a 2-row barley stem in the 6-leaf stage, showing the rachis and a side view of anthers, awns, and side spikelets. Stain has been used to mark out structures : *an*, Anthers ; *a*, awn ; *s'*, side spikelet. X 30.
- B, A 6-row barley spike from a stem in the 6-leaf stage, illustrating awn development and the comparative development of side and central spikelets : *a*, Awn ; *an*, anthers ; *s*, central spikelet ; *s'*, side spikelet ; *t*, tip of spike. X 25.
- C, Part of a barley spike from the stem of a 2-row barley in the 5-leaf stage, showing the differentiation of the tip of the spike : *an*, Anthers ; *e*, empty glume ; *e'*, empty glume of side spikelet ; *s'*, side spikelet ; *a*, awn ; *t*, tip of spike. X 25.
- D, Part of a spike from a stem in the 6-leaf stage, showing the collar at the base of the spike : *c*, Collar ; *x*, second node of the rachis. X 30.
- E, Spikelet of a 2-row barley : *pe*, Pedicel ; *s'*, side spikelet ; *st*, style ; *e*, empty glumes ; *an*, anthers ; *a*, awn. X 15.
- F, Spikelet of a 6-row barley : *s'*, Side spikelet ; *e*, empty glume ; *st*, style ; *an*, anthers ; *a*, awn. X 15.
- G, Spike of a 2-row barley : *s'*, Side spikelet ; *an*, anther. X 8.
- H, Spikelet before pollination : *r*, Rachis ; *lo*, lodicules ; *o*, ovary ; *e*, empty glumes ; *st*, stigma ; *an*, anther ; *p*, palea. X 5.
- I, Spikelet after pollination : legend as for H. (After Bonnett.)



by their structure. The internal tissues mainly consist of thin-walled chlorophyll containing parenchyma traversed by numerous inter-cellular spaces in communication with the exterior through many stomata. Schmid (1890) emphasized the importance of the awn in regard to yield. Zoebel and Mikosch (1892) established the fact that normal ears passed up to four and five times as much water as ears with the awns removed. Perlitus (1903) demonstrated that the length of the awns and the duration of the vegetative period of the spike, are inversely proportional to each other; that the grains of awned varieties tend to ripen before awnless; and that grains of awned varieties are richer in starch and ash but poorer in nitrogen than the awnless. The more recent work of Harlan and Anthony (1920) confirms these results. Removing the awns of bearded varieties lowered the yield mainly through reduction in starch content. Hooded and awnless types were normally

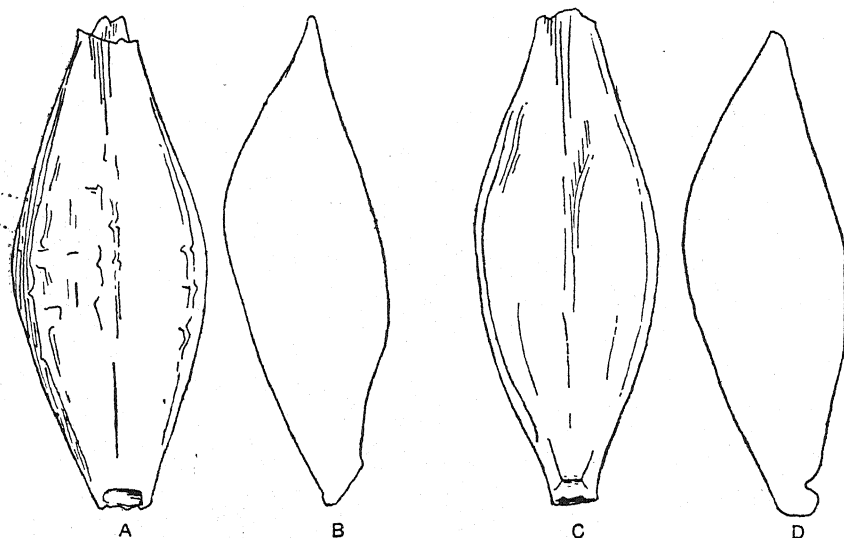


FIG. 84. Variation in shape of lemma base.

A, Dorsal view of lemma base of lax-headed barley, showing horseshoe-like depression; B, lateral view of same; C, dorsal view of lemma base of dense-headed barley, showing cross crease; D, lateral view of same. (After Wiggans.)

lower in yield than awned. Their ears also exhibited a tendency to shatter. This was apparently due to the fact that in awnless and hooded types (and in individuals whose awns had been artificially removed), an excessive amount of ash was deposited in the rachis, which consequently became brittle and readily shattered. When awns were present, much of this mineral matter passed into the awn, thus reducing the percentage of ash in the rachis. In mature awns, 30 per cent. of ash could be present; on the other hand, the rachises of clipped spikes could contain 25 per cent. more ash than the normal. (Harlan and Anthony, 1920; Harlan and Pope, 1921.)

These factors tend to show:

1. That there is an increased transpiration current due to the presence of awns.



**ANTHESIS AND POLLINATION.**—The ear of the main axis is the first to flower. The ears of the lateral axes follow in the order of their development. In any one ear, the flowers just above the middle of the axis are the first to open, followed progressively by those both above and below. In 6- and so-called 4-rowed barleys, the central flower of the triplet opens before the laterals. In any one day, two periods of maximum flowering may be noticed; the first from 6 to 8 a.m., the second and less intensive from 3 to 5 p.m. There is little or no flowering in between. Anthesis is apparently due to the rapid swelling of the lodicules. Once opened, the flower remains open for about 20 minutes. On any one spike the total duration of flowering is from 3 to 4 days. A single plant will complete its flowering within 7 to 9 days, the actual time depending on the number of tillers and weather conditions.

Certain types of barley do not open, the pollen being shed within the opened bracts. This is seen in 2-rowed erect barley, peacock barley and 6-rowed barleys. The nodding 2-rowed barleys and most 4-rowed barleys show normal opening. Under adverse weather conditions, however, blooming may take place with closed bracts in all types.

In those barleys in which open flowering is absent, cross-pollination is impossible. In 4-rowed barleys and in 2-rowed nodding barleys, cross-pollination, though possible, very rarely occurs. The explanation is to be found partly in the fact that the styles are short and rarely protrude; partly in the fact that the anthers commence dehiscence as soon as the flowers begin to open. The act of fertilization in the vast majority is therefore accomplished by self-pollination. Natural crossing appears to be very rare, but has been noted by Vestergaard (1915), Engledow (1924), Stevenson (1928) and others. Robertson and Deming (1931) found marked variability according to the variety. Five varieties showed less than 0.15 per cent. but *H. deficiens nudideficiens* exhibited up to 20.708 per cent. of crossing.

**STRUCTURE OF THE OVARY AND OVULE.**—The structure of the ovary and ovule is very similar to that of wheat. The ovary wall is composed of an outer and an inner epidermis with a middle parenchyma whose two innermost layers possess chlorophyll. As in wheat, there are two integuments in the ovule, which consists of a mass of thin-walled tissue—the nucellus. Within the nucellus there develops the embryo-sac, its internal structure resembling that of wheat.

**DEVELOPMENT OF THE GRAIN.**—After fertilization, the endosperm commences to develop almost immediately, followed by the embryo. On the outside of this endosperm, an aleurone of three (occasionally four) layers of cells forms. The nucellus is absorbed save for a single layer. The inner integument forms the whole of the testa; the outer integument disappears. The pericarp is formed from the ovary wall. Some of its tissue practically disappears, especially the parenchyma from within outwards beyond the chlorophyll layers. It is this reduction in tissue that produces the "green ripeness" of Kudelka, the chlorophyll layers being thus brought nearer to the surface. Internally, the pericarp fuses more or less with the testa. In so-called "hulled" barley, the lemma and palea "adhere" to the outer epidermis of the pericarp, a result due to the secretion of a sticky substance apparently secreted by the pericarp, which as the grain dries out more or less glues them together. In hull-less (or "naked") barley, no secretion and no fusion occur.

Several studies of the development of the grain have been published (Kudelka, 1875 ; Johannsen, 1884 ; Lerner and Holzner, 1888 ; Brenchley, 1912 ; Harlan, 1920).

After pollination, increase in length is very rapid and is completed about the seventh day. Thereafter, the lateral diameter shows its greatest increase and continues this increase until about the fifteenth day. On the other hand, the growth of the dorsiventral diameter is slower than in the case of the lateral diameter and it is maintained until nearly maturity. In the early stages, the growth is largely in the pericarp. At the same time, the tissues above the embryo-sac are stimulated, forming a tissue termed by Harlan (1920) the "ovary tip". After a few days its growth ceases and in the end it is largely absorbed.

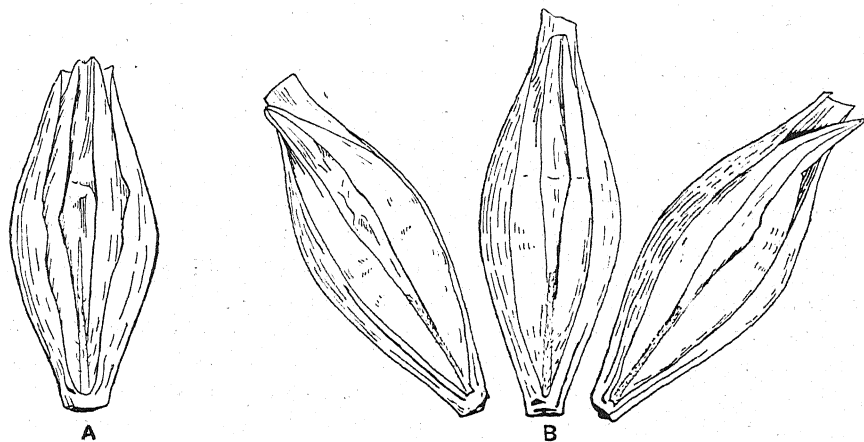


FIG. 86. Difference in appearance of ventral view, of grain of 2-rowed barley and of grain of lateral spikelets of 6-rowed barley.

A. Grain of 2-rowed barley.

B. Grain of lateral spikelets of 6-rowed barley. (After Wiggins.)

The secretion of the substance which causes the lemma and palea to adhere to the kernel occurs about the ninth or tenth day. About the fifteenth or sixteenth day, the kernel begins to toughen and the lemma begins to lose colour on the dorsal surface. This date also approximately ends the period of most rapid increase in dry matter and ash.

The percentage of water falls almost uniformly from about 80 per cent. to about 40 per cent. Brenchley (1912) gives the rate as approximately 1 per cent. a day ; Harlan (1920), under the more uniform conditions prevailing at Aberdeen, Idaho, found the higher rate of 2 per cent. A detailed study of the water relations was published by Harlan and Pope in 1923.

**MATURE GRAIN.**—The true caryopsis of barley is similar to that of wheat, but both ends are pointed. It is visible only in the so-called naked or hull-less types. In all others, it is invested by the lemma and palea.

The grains are symmetrically developed and broadest near the middle in 2-rowed barleys. (Fig. 86, A.) In 6- and 4-rowed barleys the central grains are

symmetrical and broadest above the middle; the lateral grains, however, are unsymmetrical and slightly twisted to one side, a condition more obvious in so-called 4-rowed than 6-rowed types. (Fig. 86, B.)

As already stated, the nature of the attachment of the lemma to the axis and the presence of a horse-shoe shaped depression, or alternatively, a transverse furrow at the base of the lemma, may be seen without difficulty in "hulled" grains.

In all hulled barleys, the apex of the lateral axis—the rachilla—is visible at the base of the groove. Two of its characters are of taxonomic value, viz., the length and the development of the hairs.

I. GRAIN COATS.—A. *Hull*.—Except in so-called "naked barleys" the lemma and palea fuse with the pericarp, together constituting from 10 to 25 per cent. of the grain. Structurally, both show the following four distinct layers:—

a. *Epidermis*. The cells are all silicified and are of three types:

(1) elongated cells with thick waved lateral walls.

(2) small circular cells projecting beyond the surface as low dome-shaped hairs.

(3) crescent-shaped, or circular cells occurring usually in pairs.

b. *Hypoderm*. One to 3 layers of fibres with thick porous cells.

c. *Parenchyma*. Several layers of thin-walled rectangular cells with inter-cellular spaces which are circular, elliptical or irregular.

d. *Inner Epidermis*. The cells are elongated, becoming almost isodiametric at the apex. The walls are thin and straight. Stomata may occur and, especially towards the apex, short hairs.

B. *Pericarp*.

a. *Epidermis* (Epicarp).—The cells are elongated longitudinally with the ends usually pointed or with one end truncate. The walls are of medium thickness, but not pitted. Short, thick-walled, awn-shaped hairs are found at the apex.

b. *Parenchyma*.—Several layers of cells similar to the epicarp.

c. *Cross cells*.—A double layer of cells with walls scarcely  $2\mu$  thick and varying in size from 40 to 60  $\mu$  long by 10 to 25  $\mu$  wide. A few are occasionally nearly isodiametric. Inter-cellular spaces may occur at the angles.

d. *Tube cells*.—Few in number and not distinct.

C. *Testa*.—The testa consists of two cell-layers, the outer more delicate in appearance than the inner. Its outer wall, however, is very strongly cuticularized, and presents a barrier to the entrance of water and solutes (Collins, 1918). Both layers are elongated in the same direction.

II. NUCELLUS.—The nucellus, a layer of indistinct cells, is not evident in surface view, and is regarded by many as semi-permeable. At the region of the furrow, however, it is interrupted.

III. ENDOSPERM.—a. *Aleurone layer*.—This consists of three (two to four) layers of cubical cells which contain no starch but aleurone grains. In cross-section they are more or less square; in surface view, rounded polygons.

b. *Starch endosperm*.—The remainder and vast bulk of the endosperm

consists of thin-walled cells containing both starch and protein. In translucent grains, the percentage of protein is high; in mealy grains, the percentage of starch. The starch grains are of two sizes, both smaller than in wheat.

IV. EMBRYO.—The general structure of the embryo is similar to that of wheat. The scutellum is oval and should extend well over the surface of the

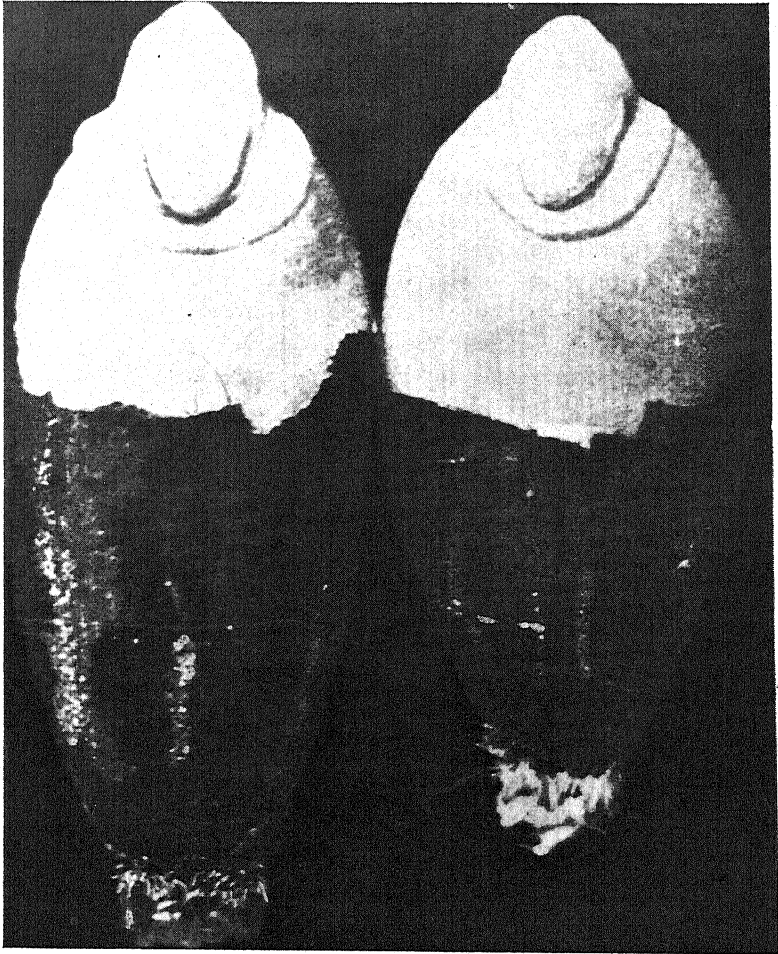


FIG. 87. Two grains of an Abyssinian barley.

A fairly well-proportioned grain with a fairly ample scutellum. (After Mann and Harlan.)

endosperm. Its epithelium consists of long narrow secretory cells. There is no mesocotyl and no epiblast. The plumule, enclosed by the coleoptile, consists of several convolute leaves protecting the morphological apex. A well-developed coleorhiza encloses the primary seminal root. In addition, 5 to 8 secondary root initials are present. Harlan states that they are probably situated at the first rudimentary node. "When eight are present, three are placed on either side and

two in front." Harlan and Pope (1925) also report the finding of 6 kernels without embryos, and a much greater number deficient in endosperm content.

**Colour of the grain.** Barley grains vary in colour through white, violet, blue, blue-grey, violet-red, brown to black, with intermediate shades. This wide variation in colour is due to the relative distribution of only two pigments; a melanin-like compound, which is black; and an anthocyanin, which is red in its acid and blue in its alkaline condition. These pigments may occur in the hulls (lemma and palea), the pericarp, the aleurone and occasionally the starchy endosperm. In the hulls and pericarp, the anthocyanin is always reddish violet, indicating acid conditions; in the aleurone it is always blue, pointing to alkaline conditions. Harlan (1914) describes the inter-play of these pigments as follows: "White denotes the absence of all pigment; a heavy deposit of the melanin-like compound in the hulls results in black; a light deposit, brown. Anthocyanin in the hulls results in a light violet-red. In naked forms the melanin-like compound in the pericarp results in a black kernel; anthocyanin produces a violet one. The acid condition of the anthocyanin in the pericarp superimposed upon the alkaline condition in the aleurone layer gives the effect of a purple colour, while a blue aleurone beneath a colourless pericarp is blue-grey. White hulls over a blue aleurone cause the grain to appear bluish-grey. Black hulls over a blue aleurone give, of course, a black appearance." The following analysis (from Wiggans) summarizes the above situation.

1. (a) Hulled varieties without pigment in either lemma or aleurone layer.
- (b) Hull-less varieties without pigment in the aleurone layer or in the pericarp.

Either of these conditions results in a white or a yellow barley.

2. (a) Hulled varieties with a blue aleurone layer showing through the superimposed lemma.
- (b) Hull-less varieties with a blue aleurone layer showing through a pericarp containing no pigment.

Either of these conditions results in a blue barley.

3. (a) Hulled varieties with purple lemmas.
- (b) Hull-less varieties with blue aleurone and red pericarp.

Either of these conditions results in a purple barley.

4. (a) Hulled varieties with black lemmas.
- (b) Hull-less varieties with black pericarp.

Either of these conditions results in a black barley.

**CHROMOSOME NUMBERS.**—The genus *Hordeum* forms a polyploid series, with 7 as the basic chromosome number.

7-chromosome group: *H. spontaneum*.

*H. maritimum*, *H. caput-medusae*.

*H. murinum*, *H. pusillum*.

*H. caespitosum* (?).

*H. gussoneum*, *H. nigrum*.

*H. nudiramulosum*, *H. nudum*.

*H. tetrastichon*.

14-chromosome group : *H. pavi.*

*H. murinum.*

*H. secalinum.*

*H. bulbosum.*

*H. silvaticum, H. jubatum.*

28-chromosome group : *H. nodosum.*

*H. arenatum.*

All the cultivated barleys, however, have been shown to belong to the 7-chromosome group (Nakao, 1911 ; Kihara, 1924 ; Stolze, 1925 ; Emme, 1925 ; Tanji, 1925 ; Aase and Powers, 1926 ; de Litardière, 1926 ; Griffée, 1927 ; Kagawa, 1929 ; Ghimpu, 1929 ; Stahlin, 1929).

Emme (1925) compared the Asiatic barleys with the African forms. In certain of the Asiatic forms he found that two of the chromosomes may possess satellites (small secondary chromosomes attached to the others by a fine thread). African forms never possessed two such satellites, but may possess one.

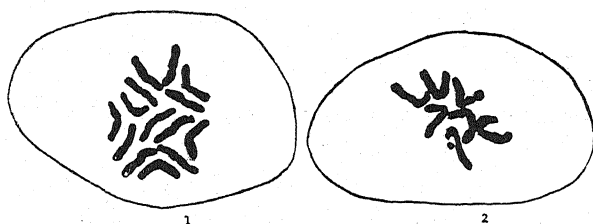


FIG. 88.

Somatic chromosomes of 1, diploid and 2, haploid barley. (After Johannsen.)

Ghimpu (1929, 1931) found that most of the cultivated barleys have  $14 + 2$  satellites. The wild barley, *H. maritimum*, has no satellites. In his last paper he considers that these satellites are merely deeply constricted portions of the chromosomes in question.

The course of somatic mitosis was studied by Inouye (1931). Blanco and Homedes (1928) studied meiosis in a variety of *H. hexastichum*, and Inouye (1931, 1933) published a detailed description of meiosis in both 2-rowed and 6-rowed varieties. No difference was found between 2-rowed and 6-rowed varieties.

Ekstrand (1932) has described partially sterile plants which, when crossed with normal, segregated into normals and partially sterile in a 3 : 1 ratio. Cytological examination showed that there was a variable amount of asyndesis at the heterotypic metaphase. Ekstrand suggests that the non-formation of bivalents may be due to a specific gene (cp. Brink in Maize).

**GERMINATION.**—Considerable attention, due to its importance in the preparation of malt, has been paid to the factors concerned in germination. The optimum temperature is said to be 68° F. The minimum lies between 37.4° to 39.2° F., and the maximum 82.4° to 86° F. By “germination energy” is meant the ability to germinate within a specified period. It is expressed as a percentage in a 72-hour period. A good malting barley at 64° F. should have a “germination energy” of 96. Harlan and Pope (1922) have shown that barley grains may germinate when taken from the plant 6 days after pollination. Their dry matter





FIG. 89. Photomicrograph of a part of the scutellum and endosperm of a germinating barley grain.

The initial stage of germination is shown. Enzymatic action has begun in front of the epithelial layer (a), but not next the aleurone (b). (After Mann and Harlan.)

then weighs about 5 mg. The seedlings are small, but produce normal though slender plants.

The greater part of the water enters the grain on germination through the base. The structure of the membranes and especially the testa, over the remainder of the grain is such that even the entrance of water is retarded for some time. Brenchley (1912) states that quite early in the development, the nucellar integument must be pricked to allow the entrance of fixing fluids. The work of Collins (1918), however, indicates that the semi-permeable membrane which barley has long been known to possess, must lie at the base of the grain. Its exact situation is uncertain, but it must lie in the neighbourhood of the coleorhiza. On the other hand, Brown (1907) concluded that the nucellar membrane functioned as the semi-permeable layer (but see also under Wheat, p. 127-128).

With the entry of the water, the radicle begins to swell, and almost simultaneously starch—previously absent in the embryo—begins to appear in the coleorhiza, the periblem of the root and in the plumule. No starch is then detectable in the scutellum. When, however, the primary root breaks through the coleorhiza, starch may be found in the cells of the scutellum immediately below the epithelium, thereafter progressing inwards. At the same time (24 to 36 hours), the walls of the empty and often partly crushed endosperm cells next the epithelium exhibit a softening and partial dissolution. The walls farther in then show a similar effect. Then and not till then, the starch grains begin to break down. Accompanying this dissolution, there is a general advance of the swelling-scutellar tissue into the endosperm. According to Brown and Morris (1890), the starch is converted into maltose, which is in turn transformed to sucrose on entering the scutellum. There is little doubt that these changes are primarily due to the secretion by the epithelial cells of a cytohydrolytic enzyme and diastase. The aleurone layer appears to produce similar enzymes. Proteases must also be present, but whether secreted by the epithelium or potentially contained in the endosperm itself, is uncertain. Harlan, however, believes that the epithelial cells are the main source of all the enzymes.

**SEEDLING.**—The primary root as noted above appears within 24 to 36 hours. It is followed by from 5 to 8 secondary seminal roots which together with the primary one form a bunch of rootlets at the base. The coleoptile appears somewhat later, delayed by the fact that it does not break through the investing lemma and palea, but forces its way upwards beneath them and thus appears first at the apex of the grain. In naked barleys, it appears much earlier.

Once above soil level, the coleoptile tip opens, and the first foliage leaf appears, followed rapidly by the second and third. These leaves are markedly twisted. The appearance of the coleoptile above ground is mainly due to elongation of the inter-nodes immediately below its insertion. The length this node may obtain depends on the depth of planting.

The young leaves of the seedling are glabrous with the nerves inconspicuous; the upper surfaces are rough; the collar is conspicuous and the auricles prominent and clasping.

Later, and generally just prior to the development of the first tillers, the first of the secondary or adventitious roots appear from a thickening node near the ground level.

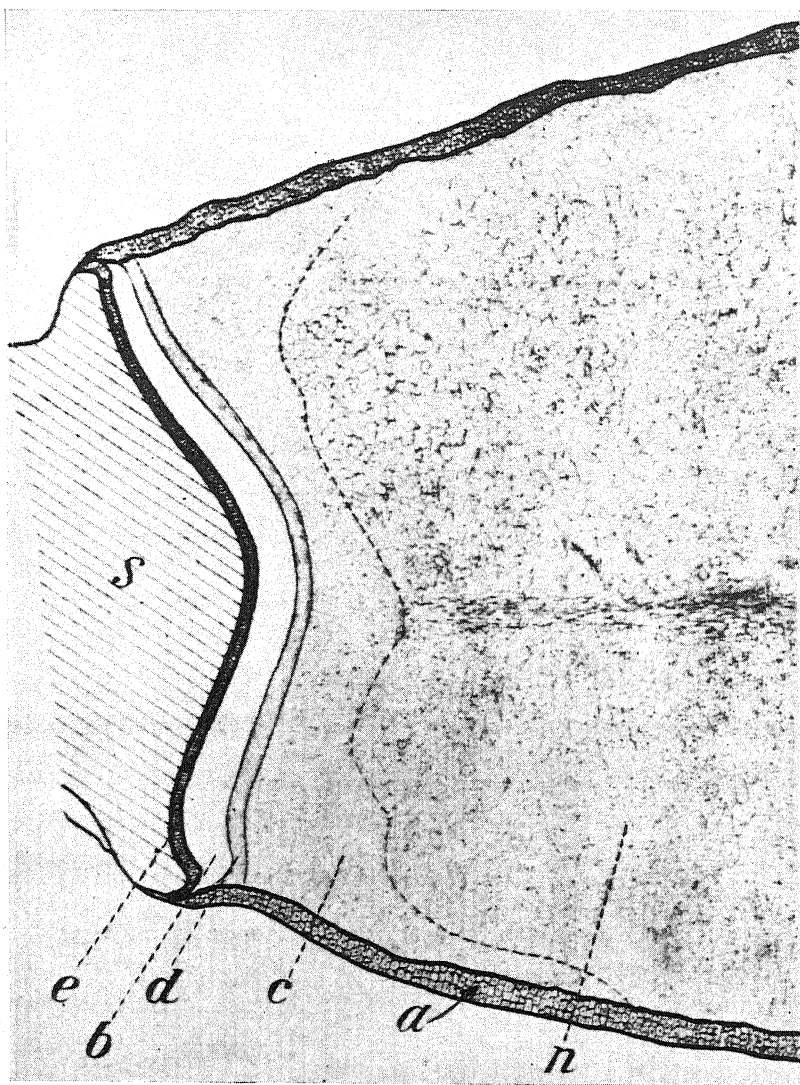


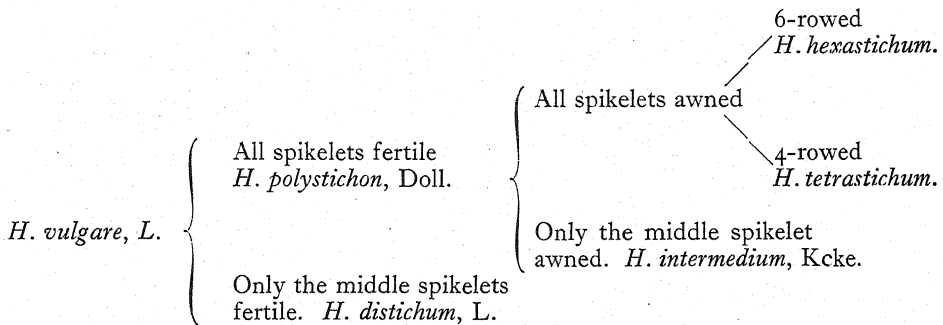
FIG. 90. Longitudinal section of barley grain, showing the stage of endosperm conversion at the end of the second day of germination.

The starch endosperm is being broken down in the dense areas directly in front of the epithelial layer, (*e*), of the scutellum (*s*), and more rapidly in the less dense areas adjacent to the aleurone layer, (*a*). *b*, Clear fluid area produced during germination; *c*, corroded area of starch endosperm; *n*, normal starch endosperm not yet attacked. (After Mann and Harlan.)

CLASSIFICATION.—Linnaeus (1748) recognized six types of barley, four species and two varieties. In analytical form these were :—

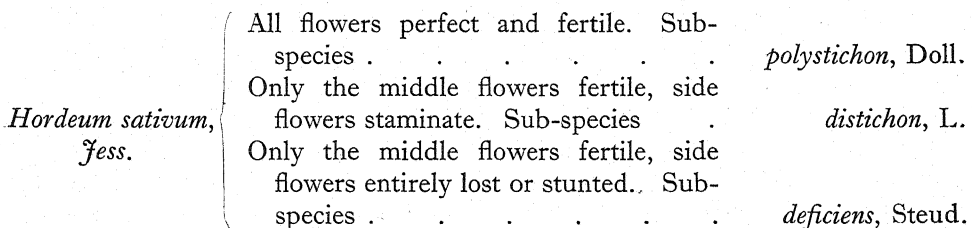
- A. All spikelets fertile.
  - B. Spikes dense. . . . . *Hordeum hexastichon*, L.
  - BB. Spikes lax . . . . . *Hordeum vulgare*, L.
  - C. Kernels hull-less . . . . . *Hordeum vulgare* var. *coeleste*, L.
- AA. Median spikelets fertile.
  - B. Spikes dense . . . . . *Hordeum zeocriton*, L.
  - BB. Spikes lax. . . . . *Hordeum distichon*, L.
  - C. Kernels hull-less. . . . . *Hordeum distichon* var. *nudum*, L.

Schübler (1818) then divided *H. distichon* into *erectum* and *nutans*. Jessen (1855) limited the species to one, which he termed *H. sativum*, Jess. Henze (1872) was probably the first to deal with fairly adequate material, and this formed a basis for the still more extended classification of Körnicke (1882 and 1885) who stressed the variety as the unit. His treatment of the major groups, however, was far from satisfactory. Following Jessen, he recognized one primary species, *H. vulgare*, L. This he subdivided into four primary groups.



A large number of varieties within these sub-species were then differentiated. His treatment as a whole is authoritative, but in view of modern genetical work his rigid nomenclature of varieties was both misleading and cumbersome.

Voss (1885) reverted to the position taken up by Jessen, and used his *Hordeum sativum* as the species name. His further analysis was into sub-species, varieties and sub-varieties.



Atterberg (1899) also referred all the forms to but one species, *H. sativum*, Jess. and made four sub-sub-species on the basis of the nature of the glume (=lemma) appendage and the size of the awn. In 1893 Bolin perfected

the Swedish system. For the first time, certain additional characteristics (in part noted by Neergaard, 1889) were stressed, viz. : the size and hairiness of the rachilla, the nature of the grain base, and the presence or absence of bristles on the lateral nerves of the lemma.

Beaven (1902) in his classification of English barleys recognized but one species (*H. sativum*, Jess.), dividing it into six groups.

- |                                   |   |  |  |
|-----------------------------------|---|--|--|
| <i>Hordeum sativum</i> ,<br>Jess. | { | A. All spikelets fertile.  |  |
|                                   |   | B. All spikelets normal.   |  |
|                                   |   | C. Spikelets wide with short inter-nodes . . . . .   | <i>hexastichum</i> , L.                                |
|                                   |   | CC. Spikelets narrow with long inter-nodes . . . . .   | <i>vulgare</i> , L. (= <i>H. tetrastichum</i> , Kcke.) |
|                                   |   | BB. Spikelets of median rows normal, spikelets of 4 lateral rows diminutive and without awns . . . . . | <i>intermedium</i> , Kcke.                             |
|                                   |   | AA. Only the median spikelets fertile.   |  |
|                                   |   | B. Four lateral rows infertile or staminate.   |  |
|                                   |   | C. Spikes wide with very short inter-nodes . . . . .   | <i>Zeocriton</i> , L.                                  |
|                                   |   | CC. Spikes narrow with long inter-nodes . . . . .  | <i>distichum</i> , L.                                  |
|                                   |   | BB. Four lateral rows rudimentary and without floral organs . . . . .                                  | <i>deficiens</i> , Seud.                               |

On the other hand Harlan (1918) again recognized four species.

- |  |                               |
|--|-------------------------------|
| A. All spikelets fertile (6-rowed barley).   |                               |
| B. Lemmas of all florets awned or hooded . . . . .   | <i>H. vulgare</i> , L.        |
| BB. Lemmas of lateral florets bearing neither awns nor hoods . . . . .   | <i>H. intermedium</i> , Kcke. |
| AA. Only the central spikelets fertile (2-rowed barley).   |                               |
| B. Lateral spikelets consisting of outer glumes, lemma, palea, rachilla and usually rudiments of reproductive organs . . . . .   | <i>H. distichum</i> , L.      |
| BB. Lateral spikelets reduced, usually to only the outer glume and rachilla rarely more than one flowering glume present, and never rudiments of sexual organs . . . . . | <i>H. deficiens</i> , Steud.  |

He then subdivided each species into eight varieties. These varieties were again separated into sub-varieties. Following earlier writers the Latin nomenclature was used throughout, resulting in the same unnecessary cumbersomeness. A particular variety may thus be designated as, *Hordeum vulgare*, L. *var. pallidum*, Seringe, sub-var. *latiglumatum*, Köcke.

Wiggans (1921) accepted Harlan's grouping, but classified the varieties without

the adoption of a cumbersome terminology and on the basis of a series of alternative but readily recognizable and constant characteristics.

The above historical outline of the classification should enable the student to determine which species (or sub-species, or variety) a particular author is referring to. This—unless the literature be available—may be a matter of some difficulty. Thus Linnaeus' species *H. vulgare* was originally one of four species, limited to those forms with lax ears, and with all the spikelets equally developed. In Körnicke's classification it was excluded altogether, the one species recognized being *H. sativum*, Jess. This also was the position taken up by Beaven. Finally, Harlan and Wiggins reinstated the species with a slightly wider connotation.



FIG. 91. Typical spikes of varieties of the Four Groups of *Hordeum Sativum*.

- A. Aequale Group (= *H. vulgare*).
- B. Inaequale Group (= *H. intermedium*).
- C. Semi-deficiens Group (= *H. distichon*).
- D. Deficiens Group (= *H. deficiens*). (After Harlan.)

Whether to accept but one species or four species is difficult to decide. All the cultivated barleys have 14 chromosomes ( $2n$ ); differentiation has been based mainly on ear-characteristics and in some instances on variable characters. Even a constant difference such as the 6-rowed and the 2-rowed habit appears to be due to either a single factor difference (Biffen, 1907 b; Gaines, 1917), or to two factor differences, with the intermedium factor hypostatic to the 6-rowed factor. (Harlan and Hayes, 1920.) Apart from the spike differences, all the forms are fairly constant in their vegetative characters.

The argument has been advanced that the number of species accepted in cultivated plants should be based on their origin, and that further analysis should be based "on the order of evolution". The first statement is "a council of perfection". Authorities differ as to whether there is one wild prototype or two, and the evidence in each case is unsatisfactory. The second statement is meaningless. As the distinction between the species is based upon one character only—fertility of the spikelets—it seems reasonable to create but one species. On the ground of priority, this species would be *H. sativum*, Jess. (Orlov, 1931, 1934; Hector, 1932.)

## ANALYSIS OF THE SPECIES.

- |                                   |   |                              |
|-----------------------------------|---|------------------------------|
| <i>Hordeum sativum</i> ,<br>Jess. | A. All spikelets fertile . . . . .  | COMPLETUM SERIES.            |
|                                   | B. Lemmas of all spikelets<br>awned or hooded, kernels of<br>all spikelets equal or nearly<br>equal . . . . .   | <i>Aequale Group.</i>        |
|                                   | BB. Lemmas of central spikelets<br>awned or hooded; lemmas<br>of lateral spikelets neither<br>awned nor hooded, kernels of<br>lateral spikelets much<br>reduced . . . . . | <i>Inaequale Group.</i>      |
|                                   | AA. Only the median spikelets fertile.  | INCOMPLETUM SERIES.          |
|                                   | B. Lateral spikelets with rudimentary reproductive organs   | <i>Semi-deficiens Group.</i> |
|                                   | BB. Lateral spikelets reduced vegetatively and without rudimentary reproductive organs . . . . .  | <i>Deficiens Group.</i>      |

## HORDEUM SATIVUM, JESS.

## A. COMPLETUM SERIES.—(All spikelets fertile.)

1. *Aequale section* (= *H. vulgare*, L. of Harlan).—The spikes are erect or nodding, either 6-rowed or more or less 4-rowed according to the relative position of the spikelets. If all the spikelets are situated at equal distances from the rachis, the ear is 6-rowed. These types are generally dense with short inter-nodes on the rachis. If the spikelets are not equidistant from the rachis, the lateral spikelets tend to overlap, some more, some less, resulting in a 4-rowed type. A majority of these 4-rowed types are less dense than the 6-rowed, and the inter-nodes are correspondingly longer. In all varieties the rachis is non-articulate. The spikelets are all fertile, sessile or nearly so. The lemmas of each spikelet are awned or hooded and if awned, the awn is usually barbed. The lateral nerves of the lemmas may be barbed or smooth. The rachillas are hairy. The kernels of all the spikelets are nearly equal in size, but those of the lateral spikelets are more or less twisted. A thrashed sample may therefore be identified by the fact that the unsymmetrical grains will be double the number of the symmetrical. In

shape, the grains may be long and slender or short and plump. Hulled and hull-less varieties are to be found and there is a wide range in colour types.

The varieties may be separated with comparative ease on the basis of the characteristics used by Wiggans. These differentiations are as follow :

- A. Whether the grains are hulled *or* hull-less.
- B. Whether the lemmas are awned *or* hooded.
- C. Whether the grains are black *or* not black.

D. Whether the spikes are lax with the grains (in hulled forms), possessing a horse-shoe shaped depression at the base, *or* the spikes dense with the grains possessing a transverse furrow at the base. For further data the student should refer to Wiggans' *Memoir* (1921).

2. *Inaequale section* (= *H. intermedium*, Kcke.).—It has been generally accepted that most, perhaps all, of the varieties of this group are of hybrid origin.

In most species, the spikes are lax and nodding with the rachis articulate. The spikelets are sessile, in groups of three at each node and all fertile. The lemmas of the central or median spikelets are awned or hooded ; those of the lateral spikelets are neither awned nor hooded. The grains of the *central* spikelets are normal in size and relatively large ; the grains of the *lateral* spikelets are small, one half to two-thirds as big as the grains of the median spikelets. This is the most essential difference between the *inaequale* group and the *aequale* group, where all the grains are equal in size. Hulled and hull-less forms are known, and there is a considerable range in colour types.

None of the varieties is of much economic importance.

#### B. INCOMPLETUM SERIES.

The essential difference between this and the former lies in the infertility of the lateral spikelets. As a consequence—except in the very rare and probably abnormal instances of reduplication—the ears are 2-rowed.

1. *Semi-deficiens section* (= *H. distichon*, L.).—In this group, the lateral spikelets have normal but narrower glumes ; the lemma and palea are reduced in size ; the reproductive organs are present but rudimentary.

The spikes may be lax or dense, erect or nodding. The lemmas are either awned or hooded, with the lateral nerves barbed or smooth. The rachillas vary in length and may be long-haired or short-haired. The grains are equal in size, their broadest diameter being approximately at the middle of the grain. Lax forms have grains with a transverse furrow at the base ; dense-eared forms tend to develop a horse-shoe depression. All forms of grain colour are met with.

All the varieties falling within this section may be differentiated by using the same series of contrasting characteristics as for the previous sections.

The finest malting barleys such as Hanna, Chevalier and Archer among the nodding lax forms, and Goldthorpe and its many allied types among the erect, dense forms, belong to this section. They tend to develop grains with a thin hull and a somewhat mealy texture. Their protein content is low and the scutellum spreads well over the endosperm. The longitudinal diameter is relatively short and the transverse diameter relatively long.

2. *Deficiens section* (= *H. deficiens*, L.).—Here the lateral spikelets are not only sterile but markedly reduced. Reproductive organs are never present ;



glumes, lemma and palea are much smaller and in some cases only the outer glume remains.

The varieties are few in number and of minor economic importance. Their centre of diversity appears to be Abyssinia and they may again be differentiated on the same basis as before.

**ORIGIN OF CULTIVATED BARLEY.**—No satisfactory explanation of the origin of cultivated barleys has been advanced.

Körnicker considered that *Hordeum spontaneum* was the wild prototype. It is related to the 2-rowed drooping types, which he regarded as derived therefrom, possibly by mutation. A shortening of the spike axis produced 2-rowed erect types; a still greater shortening accompanied by an enlargement of the basal grains, gave the dense-eared types. Four-rowed and 6-rowed barleys he derived from the above three forms respectively by the lateral spikelets becoming fertile.

Rimpau (1892) practically reverses the above. He regarded 6-rowed types as primitive, and derived the others therefrom by a process of sterilization of the lateral spikelets.

Schulz (1913) in part follows Körnicke. He argued that the wild species *H. spontaneum* gave rise, by the accumulation of several small mutations, to the new wild form, *H. ischnatherium*, widely distributed in the Tigris-Euphrates region. This species varies in the character of its lateral spikelets, but in general is nearer the 6-rowed types than *H. spontaneum*. As a consequence he believed that the cultivated 6-rowed barleys were derived by further variants from this species; the 2-rowed barleys by variants from the original *H. spontaneum*. The deficient forms were believed to be derived directly from *H. spontaneum*, not indirectly from cultivated 2-rowed derivatives; and the intermediate forms were treated as crosses between 6-rowed and 2-rowed types.

None of the theories takes into account the fact that the scutellum of cultivated barleys has a double bundle, whilst that of the wild type has but one.

Leaving out the morphological speculations, more precise data can be obtained from the study of distribution.

Orlov (1934) has shown that there are two primary centres of diversity: Abyssinia and Eritrea on the one hand, China and Japan on the other. The common cultivated forms of N. Africa, Europe and Russia, have come from the East, more immediately from Asia Minor, Palestine, Syria, Pamir, Persia and Afghanistan.

The barleys of Abyssinia are little known, but they constitute a distinct series including a vast wealth of forms, which are apparently still in process of evolution.

Historically, barley is a very ancient crop. Thus Jackson (1933) states that stores of wheat and barley recently found in Egypt must have been grown between 5,000 and 6,000 B.C. One specimen consisted of 57 per cent. of 6-rowed barley, 23 per cent. of 2-rowed barley and 20 per cent. wheat. The types present were practically identical with those cultivated in Egypt at the present day.

**INHERITANCE AND HYBRIDIZATION.**—Genetical studies within the varieties have been conducted on a considerable scale. The more important of these have dealt with such characters as sterility, density, the hulled condition,

awning, the hooded character, glume characters and colours, colour of grain, etc. Some of these have been referred to in the text.

So-called winter barleys (in contrast to spring barleys) have generally a compact "winter habit" of growth. They are said to contain more sugar than spring forms (Yasuda, 1926; 1927); also they germinate at lower temperatures and have a slower rate of absorption. (Satô, 1929.) Vavilov and Kuzneksova (1921) obtained winter forms out of crosses between two spring forms. Takahasi (1924, 1925) found that the spring form was dominant over the winter form, but intermediate pseudo-winter forms occurred. Schiemann (1925) then showed that the winter hardiness and the winter growth habit were independent of one another. Kuckuck (1929) corroborated this conclusion and found that plants with "winter habit" only did not survive the winter; and that there was a correlation between the growth habit and the length of the vegetative period. Huber (1932) in a study of crosses between 2-rowed winter barley and a spring barley was led to postulate the existence of four factors. True winter barleys are recessive for all four factors for heading, but spring barleys must contain at least three of the factors in the dominant condition. Kuckuck (1933) in a further study found that a three-factor basis was insufficient to explain the results. He now believes that winter-habit, hardiness and late earing are all closely correlated, and cannot be regarded as distinct phenomena.

A general review of the genetical position is to be found in Hayes and Garber and in the *Barley Breeding Bibliography*, Imp. Bur. Plant Gen. (1930). (See also under Vernalization in Wheat, p. 138.)

Seven linkage groups have been discovered (Kuckuck, 1930; Buckley, 1930; Robertson, 1932 and 1933; Wexelsen, 1934).

A limited number of mutations have been reported (Schneider, 1913; Kiesseling, 1912 and 1918; Vestergaard, 1921; Scharnagel, 1925; Schiemann, 1930). Induced mutant forms, chiefly chlorophyll defects, have been obtained through the action of X-rays and radium by Stadler (1928).

Practically no inter-specific hybridization has been carried out. Mallock (1921) succeeded in crossing *H. vulgare* and *H. murinum*. The two F<sub>1</sub> plants obtained died as seedlings. Kuckuck (1934) obtained with difficulty a single plant from the cross *H. sativum* ♀ (n = 7) × *H. bulbosum* ♂ (n = 14). It resembled *bulbosum* but was quite sterile.

**ECONOMIC USES OF BARLEY.**—The predominant use of barley is in the preparation of malt. A limited amount of flour is also made from it. "Pearl barley" is shelled barley. The grains are also used as stock food, and the whole plant for hay and as a green food. For this purpose the so-called hooded barleys are mainly grown in South Africa.

The Production of Malt. Mann and Harlan (1915) who made a special study of the barley grain with reference to its enzyme-secreting areas, summarizes the characters of an ideal grain as follows:

"It is broadly oval with a scutellum extending well over the edges of the adjacent endosperm. The greatest vigour is found in a grain possessing an epithelial layer of long narrow cells; the highest condition of efficiency in a grain which is well matured and well cured. If a large yield of malt is required, the

size of the grain should be large ; if diastase be the main consideration, the size should be smaller."

The grains are first steeped in water for about 48 hours. They are then spread out and allowed to germinate at a temperature between 50° and 60° F. Germination proceeds until the primary roots, but not the coleoptiles, are visible. Further germination is then stopped by drying out the grains in a kiln. The resulting product is malt. This malt is then ground, mixed with water, and incubated for some time at a suitable temperature. During this mashing process the enzymes activated by the preliminary germination convert, on the one hand, the starch into maltose and dextrin (diastatic action), and on the other hand, the insoluble albuminoids into soluble albuminoids (peptase action). The resulting product is wort. The wort is then boiled, hops added and the whole fermented by the addition of yeast.

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## CHAPTER VII

### RICE—ORYZA SATIVA, L.

RICE belongs to the collective species *Oryza sativa*, and the following description is therefore generalized, based on the more important of the cultivated forms.

The rice plant is an annual cereal, very variable both in habit and habitat. The chief differences in habit are dealt with in the text. As regards habitat, rice is essentially tropical, but it may yet grow successfully—(a) as mountain rice, *e.g.*, at an elevation—though still under humid conditions—of 6,000 feet on the Himalayas; (b) as semi-tropical rice in Spain, Italy, California, etc.; (c) as irrigated or flood-water tropical rice; (d) as deep-water rice, essentially tropical.

Even in one cultural district, the crop may be sown and harvested at different times and under very different conditions. Thus in Bengal, five main crops can be distinguished:

1. *Highland Aus*, sown broadcast in April-May, and harvested August-September. 2. *Transplant Aman*, sown in seed beds in June, transplanted in semi-lowland in July-August, and harvested in November-January. 3. *Lowland Aus*, sown broadcast in lowland in February-March, harvested in August-September, and growing in 5 to 6 feet of water. 4. *Lowland Aman*, sown as number 3, but on still lower areas and harvested in December-January, some capable of growing in 30 feet of water. 5. *Boro*, sown in seed beds in October, transplanted in December on areas which never dry, and harvested about March (Hector, 1934). Parallel situations can be found elsewhere.

**ROOTS.**—a. **SEMINAL ROOTS.**—On germination the coleorhiza appears at the base of the grain as a small glistening knob, which is soon ruptured by the primary seminal root. Two additional roots then develop almost immediately, both of which may be preformed. All three may later form short laterals. To what extent these seminal roots may grow and for how long they may function, do not appear to have been ascertained.

b. **SECONDARY ROOTS.**—The secondary roots arise endogenously from lower nodes of the young plant and its tillers. Their number increases until about the time of the elongation of the stem, after which few new roots are said to develop (Copeland). As new roots form the older roots are stated to die off progressively from the base. According to Herrero (1919), the dry weight of the roots may even decrease after the panicle appears.

Copeland (1924) found the average number of roots on 10 thirty-four-day-old plants of the variety French to be 16, and the average length of the longest root 15.6 cm. On an older plant of "French" (precise age not stated) with 10 culms, the maximum number of roots present was 20.2. The longest roots found varied from 18.5 cm. to 40.1 cm.

More precise data is given by Sethi (1930) who studied the root system of four varieties, both in pots and in the field.

At the end of a fortnight's growth, two distinct types of root were present : long, flaccid, light brown and much branched roots accompanied by comparatively short, thicker, unbranched roots of a white waxy appearance. These short roots probably correspond to the so-called "white roots" of barley. They also exhibited their maximum development in clay. Later, the white roots altered for, about a month and a half after sowing, they began to branch and became weak and flaccid. Generally speaking, the white roots increased in number from the fifteenth day to the time of the appearance of the flowers. At maturity all the roots were thin, branched and flaccid.

In pots, the penetration ranged from 10 to 18 inches at the beginning, and reached a maximum of 2 to 4 feet after flowering. The majority of the roots were found within the first foot of the soil. During the early stages, the development of laterals was poor ; after a month and a half they developed extensively. Very fine laterals also developed near the crown of the plants on the soil surface.

In the field the root system was similar to that in pots, but on the whole was less extensive. The roots also ran more horizontally and never attained the same vertical depths.

The root system as a whole was influenced by the soil texture, the water and air supply and by the manurial system. Further, each variety tested exhibited a characteristic root system. In the early varieties the system was less well developed than in late varieties ; also in coarse-grained varieties the root system was coarse in texture whilst in the fine-grained varieties, the system was much more delicate.

In the different series, characteristic root colours tended to develop. Thus in clay the roots were a bright red colour ; in soils treated with ammonium sulphate the colour was a dull red brown ; in superphosphate, the red colour was found only on some roots near the crown ; in soils treated with farmyard manure, and in gravel and in sand, the roots were uncoloured. According to Kadam (1934), the roots of a Burmese variety turn red on exposure to light. The character behaves as a dominant to colourless.

In the deep-water rices, whorls of adventitious roots may form at the nodes above ground level.

**ANATOMY OF THE ROOT.**—In the young root there is an epidermis of thin-walled cells, more or less square in outline. Towards the apex these cells may grow out to form the root hairs. Beneath the epidermis and separated therefrom by a single layer of thin-walled cells is a single layered exodermis of thick-walled cells. The remainder of the cortex consists of large thin-walled cells exhibiting a fairly distinct radial arrangement. Its innermost layer constitutes the endodermis which exhibits an early development of the casperian strips.

The central cylinder is at first unligified and at an early stage develops a number of very large central vessels—either a single central vessel or six vessels arranged starwise. To the exterior, groups of smaller vessels alternating with phloem and separated by thin-walled parenchyma, form a vascular ring. The xylem of these groups abuts on a single layered pericycle. The remainder of the cylinder is constituted of thin-walled parenchyma.

As the root ages, the epidermis and the layer immediately beneath are sloughed and the exodermis replaces them. This layer then thickens further and its outer walls become suberized. Thickening of certain of the adjacent layers of the cortex

may follow. Simultaneously, the radially arranged intermediate cells of the cortex separate from one another and alternate strands or groups of strands so formed may shrivel and die. There is thus formed a cortical structure strongly resembling that of many water-plants. Adjacent to the endodermis, which gradually thickens, two to three layers of cortical cells tend to remain more or less unaltered. At maturity the central cylinder is thus invested by a loosely pleated jacket-like cortex.

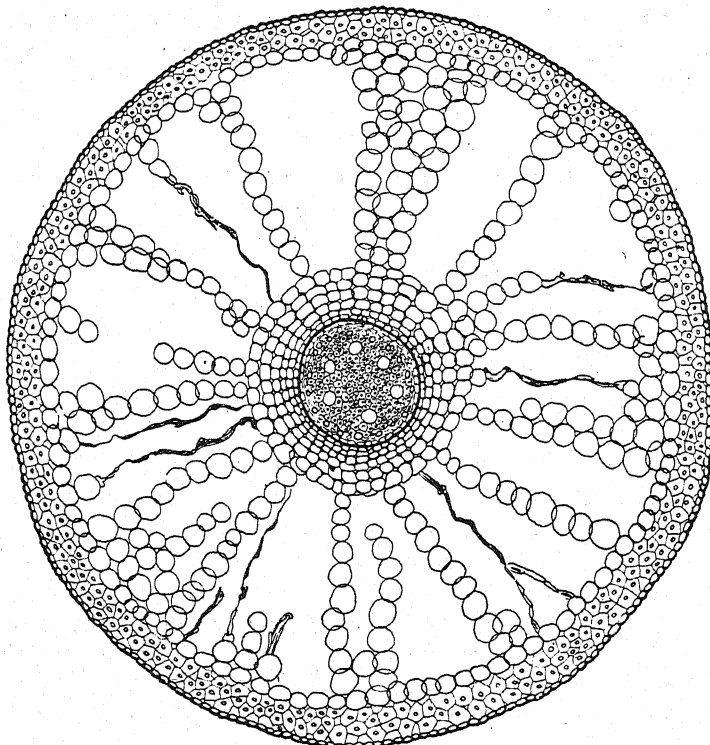


FIG. 92.

Transverse Section of Mature Root, showing modified cortex. (X 180.) (After de Haan.)

The central cylinder also becomes modified. The vessels become more lignified, and in time the cells of the parenchyma are strongly thickened, thus forming a solid central core to the root.

**STEMS.**—The main axis of the stem is differentiated from the growing point of the embryo, enclosed at first by the coleoptile. The ultimate height attained depends on the number of inter-nodes and the environmental conditions. The number of inter-nodes may vary from about 10 to a maximum of 20. Generally speaking, very early strains and short duration strains have low numbers, whilst in very late strains and long duration strains the numbers tend to be high. Exceptions, however, are known.

In very early stages there is little difference in height between varieties. Later, elongation is continuous and reaches a maximum when the plants are flowering. ✓ Short duration varieties in general grow much more rapidly than long

duration and late varieties. In the variety French, studied by Copeland, elongation of the first 3 inter-nodes was but slight. The growth of the fifth inter-node was considerable. Thereafter the inter-nodes from the sixth to the thirteenth grew out in rapid succession from the 30th of July to the beginning of August, the lengths attained being approximately equal. There is, however, a tendency for the inter-nodal lengths to increase from the base upwards. This is most marked in the uppermost inter-nodes. Thus, the fourteenth, fifteenth and sixteenth inter-nodes were successively longer and their duration of growth also greater. The terminal inter-node—the peduncle—carries the panicle and is the longest of all. In deep-water rices, length of inter-nodes is dependent on the water depth. The ultimate height attained is a varietal characteristic and varies from approximately 18 inches to 70 inches.

The culms so formed are more or less erect, cylindrical and hollow, except at the nodes, and vary in thickness from about 6 to 8 mm.

The nodes are clearly defined by the presence of a distinct thickening, the pulvinus, immediately above the actual node. This pulvinus may be coloured or colourless, the colour varying in intensity up to a deep uniform purple. Colour in the pulvinus is always associated with colour in the leaf sheath, but the converse is not found. The inter-nodes may also be green (colourless) or coloured. The pigment in coloured forms may be diffused in the epidermis or in the parenchyma or confined to the bundle sheaths in the form of coloured streaks or in various combinations of these. It may also appear early or late in the development and is either temporary or permanent. Inter-nodal colour has always been found to be dominant to colourless, and either one, two or three factors are implicated, giving 3 : 1, 9 : 7 or 27 : 37 ratios respectively.

Inheritance studies of height indicate that one or several factors are concerned. Shortness may be a simple dominant to tallness or tallness may be a simple dominant to shortness. In complicated cases the evidence indicates a multiple factor explanation (Ramiah, 1933<sup>a</sup>). Ramiah (l.c. and 1933<sup>b</sup>) also found a correlation between height and flowering duration. The evidence so far indicates that this correlation is positive in early varieties and negative in late varieties. These two characters were also found to be associated with other characters such as length of ear and emergence of ear, and very definitely associated with yield, "the later and taller plants giving a very much increased yield over the earlier and shorter plants."

A bud may form in the axil of each leaf of the main stem, but normally, only the lowermost buds from the crowded nodes at ground level develop into branches. As a consequence a typical "tillered" plant develops.

The number of tillers produced is approximately constant for any one variety under comparable conditions. If the seed is not sown too deeply, tillering commences about 15 days from the sowing date: it may continue for a short period or be distributed over a considerable part of the growth period. If the tillers are few in number and produced within a short time period, ripening of all is approximately equal: if numerous and (or) produced discontinuously over a lengthy period of the plant life, a variable number of unproductive tillers must result. The mean number of tillers on the more valuable economic strains may vary from 7 to approximately 12 per plant.

The number of inter-nodes on a branch is definitely fewer than on the main axis, and progressively fewer on successive branches though none has fewer than 5 to 6. In the variety French, studied by Copeland (l.c.), the first tiller had 5 inter-nodes; the fifth but 6. The first inter-node of a tiller is always short; the remainder elongate progressively to such an extent that the first formed tillers equal approximately the length of the main axis.

In some varieties the stems are more or less stiff and the resulting habit compact; in others, the stems are more prostrate and the habit "spreading". Ramiah (1930) found that the "compact" habit behaved as a simple dominant to the "spreading" habit. In plants with compact habit the basal inter-nodes were always short; in those with the spreading habit the basal inter-nodes were definitely longer, and the tillering succession more obvious.

Lodging is frequently observed in rice. In deep-water rice where, as the water recedes, the stems are too weak to support the panicles, it is a constant feature; in dry-land and irrigated types it is a variable phenomenon. Here, as in other cereals, the factors are both external and internal. The external factors that tend to promote lodging are similar to those operating in the case of wheat and other small-grained cereals (see pages 23, 101-103): the internal factors are specific to the variety. In general, somewhat stout, short strawed varieties are the more resistant, but certain of the long strawed types may be as resistant. According to Bhide and Bhalariao (1927), the more resistant types have stems with a thicker band of sclerenchyma at the periphery than lodging strains, more numerous fibro-vascular bundles, and exhibit in particular a narrow layer of small sclerenchymatous cells behind the air cavities, more or less linked to the sclerenchymatous sheaths of the bundles which lie between these cavities. These layers are generally absent in varieties prone to lodge.

**ANATOMY OF THE STEM.**—The stems are hollow except at the nodes. In transverse section, the young epidermal cells are somewhat square in outline, though much elongated when viewed from the surface. Later, these cells become much thickened, cicularized and impregnated to a varying degree with silica. To the interior the ground parenchyma is at first uniformly thin-walled, somewhat angular in outline and closely packed. In contact with the epidermis the cells are comparatively small, then rapidly increase in size, attaining their maximum at or beyond the inner ring of fibro-vascular bundles and thereafter decreasing in size until the hollow centre is attained. In the neighbourhood of the stomata they contain chlorophyll. As the stem ages, the cells immediately beneath the epidermis become strongly thickened to form a band, varying in width, of sclerenchyma in which the outer zone of vascular bundles may be included or in contact. In some varieties, as already noted, a narrow band of small-sized cells may border the inner margins of the air-cavities, and are frequently more or less continuous with the sheaths of the inner bundles. These air-cavities are always conspicuous in deep-water varieties, but vary markedly in their development in all other types.

The fibro-vascular bundles of the rice plant show considerable regularity in their distribution. The outer zone consists of small bundles which in time may be more or less included in the sub-epidermal sclerenchyma or in direct contact therewith. Beyond the outer zone a median zone of bundles occur, often situated at levels between the air-cavities. The inner zone consists of fairly large bundles,

evenly spaced and often forming a distinct ring. Each bundle is of the typical cereal type with three large vessels.

**LEAF.**—The number of leaves borne on an axis is equal to the number of nodes. Since the number of nodes on the tillers is progressively fewer than on the main axis, the leaf number on a tiller is correspondingly lower.

The first leaf of the plant is the sheathing leaf or coleoptile. The second leaf emerging through the lateral slit of the coleoptile

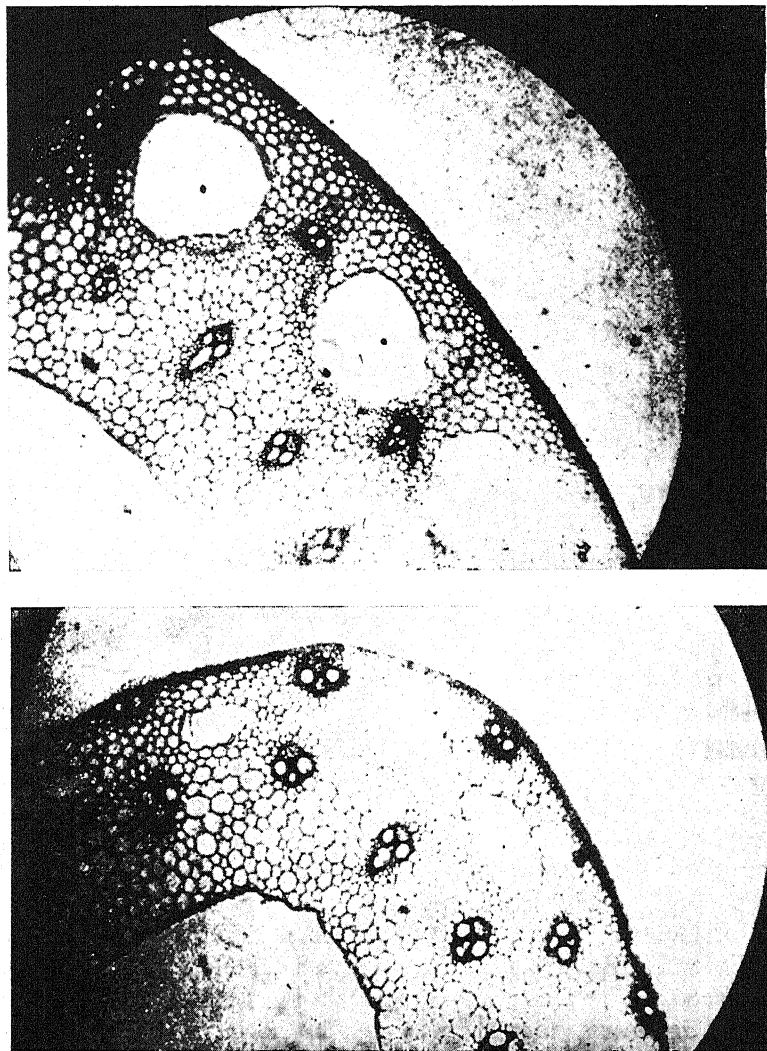


FIG. 93.

- A. Transverse section of a standing strain. Note the small-celled thick-walled cells (sclerenchyma) behind the air cavities.
- B. Transverse section of a non-standing strain, showing the absence of sclerenchyma. (After Bhide and Bhalerao.)

is reduced in size and has practically no blade. The remaining leaves are normal, except the uppermost or "flag", which is slightly modified. In every instance, the bud—a potential tiller—is enclosed in a prophyll. The normal vegetative leaf exhibits sheath, ligule, auricles and blade.

a. THE SHEATH.—The sheath is always present, encircling the whole or part of the inter-node from the pulvinus upwards. At the base the sheaths tend to exceed the length of the inter-nodes and as a consequence enwrap the base of the succeeding sheath to a variable extent. From the tenth leaf upwards, however, the inter-nodes are longer and the sheaths relatively and progressively shorter than the inter-nodal length. Growth of the sheath is mainly from the base and may

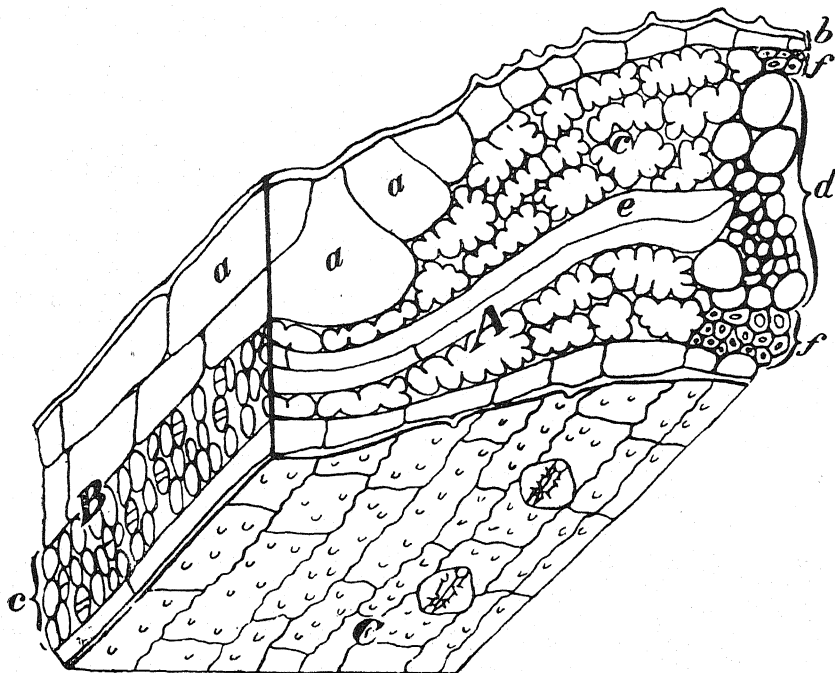


FIG. 94.

Diagram of portion of rice leaf showing : A, Cross and B, longitudinal section and C, surface view of lower epidermis : a, Motor-cells ; b, upper epidermis with papillae ; c, armed type parenchyma cells ; d, fibro-vascular bundle ; e, transverse bundle ; f, sclerenchyma cap. X 560. (After Tullis.)

continue after the blade has attained approximately its maximum length. Each sheath is split to the base, finely ribbed and more or less glabrous. The thickness and persistence vary with the variety. Colour is frequently present in the sheath, and varies in a manner similar to that found in the inter-node. When present it may be confined only to the base or be distributed throughout the sheath length and be visible either on the outer surface or the inner surface or both surfaces. The actual pigment occurs in the epidermal cells, in the tissue surrounding the bundles, or distributed throughout the parenchyma. Presence of pigment is always a dominant, but segregation ratios of 3 : 1, 9 : 7, 27 : 37 and 15 : 1 have been obtained (Hector 1922 ; Graham, 1913).

According to Graham, sheath colour is always associated with colour in the apiculus, but strains are now known in which this correlation is absent.

b. **The Ligule.** With very rare exceptions, all rice varieties have a well-developed, thin membranous ligule, tending to split as it develops. It may be colourless or coloured a faint pink to purple. If the ligule be coloured, the sheath is always coloured (Hector, 1922).

c. **THE AURICLES.**—The auricles are situated at the junction of the sheath and blade, and are somewhat sickle-shaped in outline, up to 3 mm. in length. Long slender teeth are normally present on the convex face of each. Colour is frequently present and when present is correlated with the colour of the pulvinus. Further, if the auricles are coloured the sheath is coloured but not *vice versa*. In some strains, the auricles are absent.

d. **THE BLADE.**—The leaves are long and narrow, usually slightly pubescent with a distinct mid-rib, but varying markedly in length.

In many varieties the leaves are coloured. If present, the colour is usually concentrated in the mid-rib region and on the margins, though very rarely the whole leaf is coloured.

The uppermost leaf or "flag" of the axis possesses a blade which is always shorter and broader than the lower leaves. As the panicle emerges through its sheath, its blade is wellnigh parallel to the panicle axis. After the panicle has emerged the blade falls, standing ultimately either at an acute angle to the axis, more or less horizontal thereto or definitely drooping.

A number of chlorophyll deficient mutants are known and have been studied genetically by Takezaki (1923), Kondo *et al.* (1925), Ramiah (1930) and others.

**ANATOMY OF THE LEAF.**—The structure of the leaf has been briefly dealt with by van Breda de Haan (1911), Arber (1934) and Tullis (1935).

The leaf sheath is characterized by the presence of large air-spaces in the mesophyll. The bundles are alternatively large and small and are situated just below the outer epidermis. At the base of the blade, the air-spaces are still prominent and small bundles—irregularly orientated—appear on the upper surface.

In the blade proper the structure differs considerably from that of the sheath and base. There are no large air-spaces. Rather large sub-stomatal chambers, however, occur, most evident in longitudinal and tangential sections. The parenchyma is closely packed and in cross-sections exhibits practically no inter-cellular spaces. If, however, the structure is studied in longitudinal and transverse sections the inter-cellular spaces are much more distinct, and may extend from the upper to the lower epidermis and occur in bands on each side of the bundles.

The parenchyma of the leaf is of the so-called "armed type", now known to occur in a number of grass species. In cross-sections these "armed cells" are irregularly rectangular in outline with distinct invaginations. In longitudinal sections, the cells appear to be either rectangular or elliptical and at times seem to consist of numerous small cells, the invaginations near the periphery simulating cross walls. (Fig. 94 (c) and 95 (a)).

The bundles—of the usual grass type—show a regular espacement—the large bundles being separated from one another by a number of small bundles. Each bundle has a distinct sheath and tends to be girded both above and below.



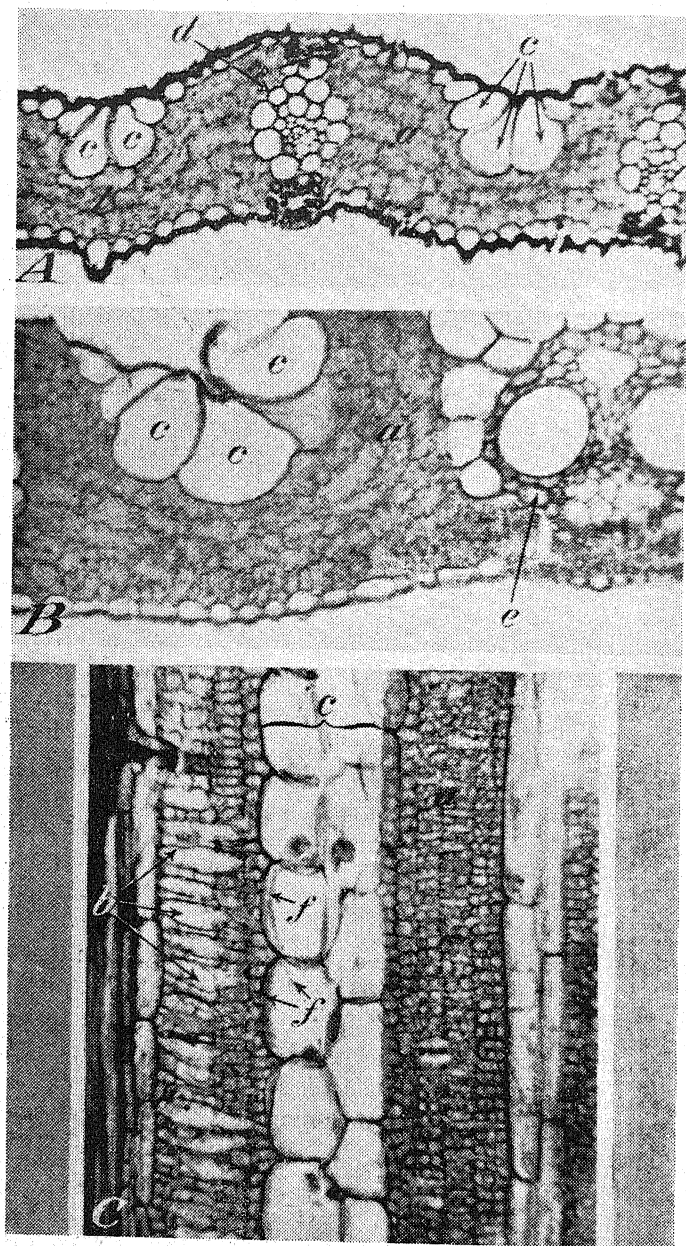


FIG. 95.

Cross-section of portion of leaf of *A*, Shoemed and *B*, Blue Rose rice, and *C*, tangential section of portion of leaf of Blue Rose rice: *a*, Armed-type parenchyma cells; *b*, intercellular spaces; *c*, motor-cells; *d*, small bundle; *e*, large bundle; *f*, hyphae of *Helminthosporium oryzae*. All X 288. (After Tullis.)

The epidermis on both surfaces exhibits considerable specialization. On either side of a fibro-vascular bundle there is a row of suberized cells alternating with cells which include a saddle-shaped siliceous deposit. A band of long cells with stomates follows, succeeded by a strip of long cells whose ends are separated by pairs of cells, a siliceous cell towards the leaf apex and a suberized cell towards the leaf base. The long cells have distinctive ripple walls, and hairs of varying type and short papillae are common. The bulbiform or motor cells occur midway between the bundles on the upper surface. (Arber, 1934 ; Tullis, 1935.)

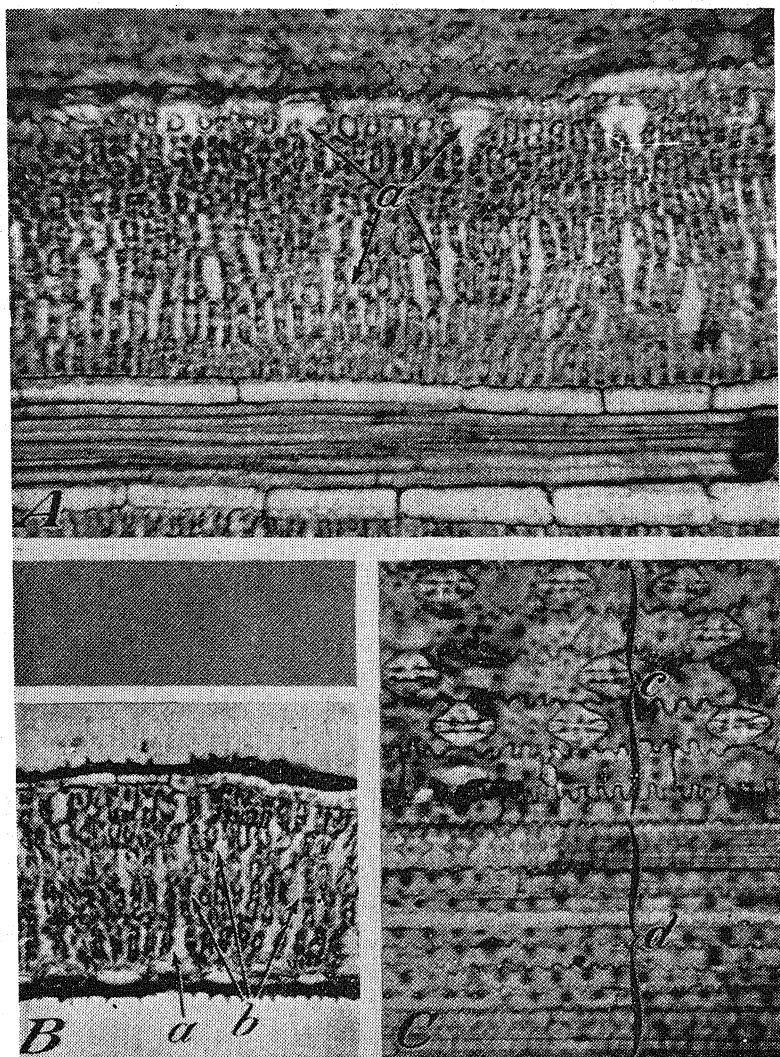


FIG. 96.

Tangential (A) and longitudinal (B) sections of portions of leaves of Shoemed and Blue Rose rice, respectively, showing substomatal chambers (a) and intercellular spaces (b); and surface view (C) of portion of leaf of Shoemed rice showing lower epidermis covering parenchyma (c) and a large bundle (d). All X 320. (After Tullis.)

**THE INFLORESCENCE.**—The inflorescence of rice is a terminal panicle borne on the peduncle or topmost inter-node. This peduncle is partly enclosed by the leaf sheath, and its length, measured by the distance from the top of the leaf sheath to the ciliate scar at the base of the peduncle, determines the exertion.

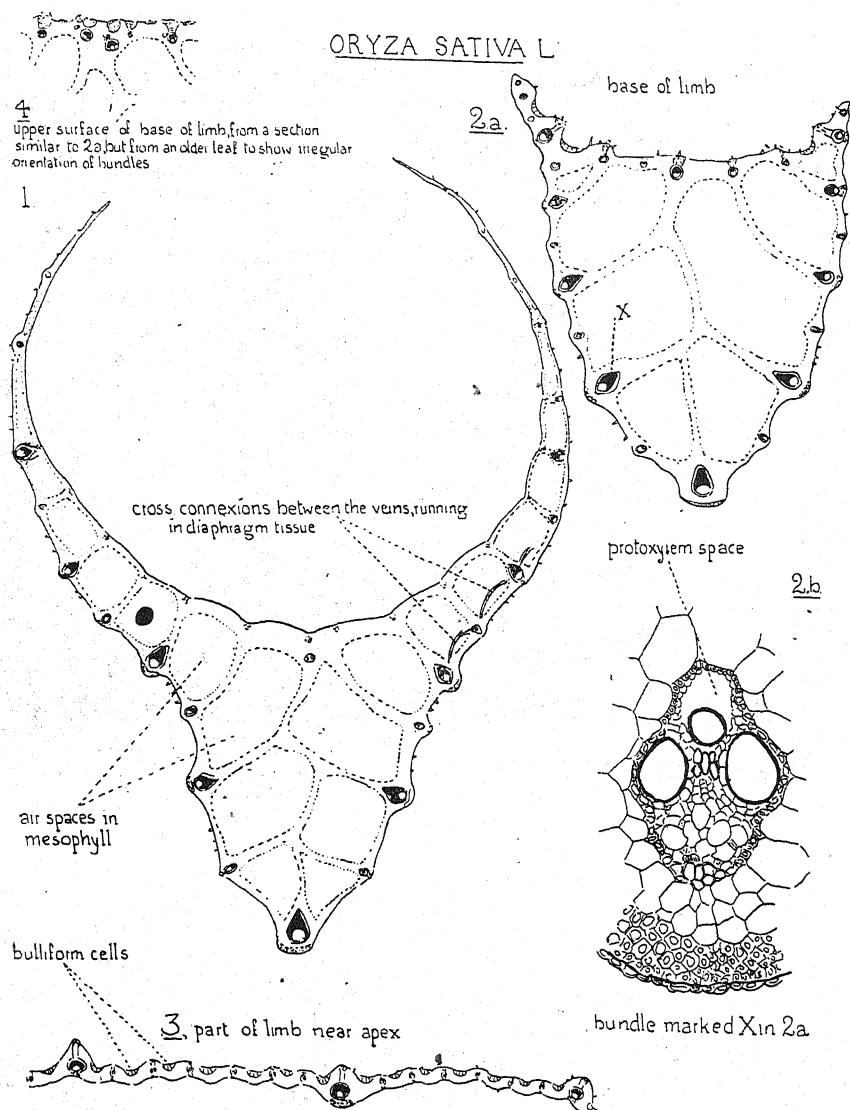


FIG. 97.

*Oryza sativa* L., leaf structure. 1 and 2a, Transverse sections of sheath and base of limb above ligule (X 23). 2b, Bundle X in 2a (X 193 circa). 3, Part of transverse section of limb near apex (X 23). 4, Part of upper surface of a transverse section of the base of a limb similar to 2a but from an older leaf (X 14) to show that some of the upper bundles are irregularly orientated. (After Arber, *The Gramineae*, by permission of the Cambridge University Press.)

The range found passes from (1) no exertion—when the scar is invisible ; (2) just exerted—when the scar is just visible ; (3) medium exertion—when the distance is half the length of the inflorescence, to (4) far exerted—when the distance is more than half the inflorescence length. An extreme condition is found in certain rare types, where the panicle is completely enclosed in the leaf sheath.

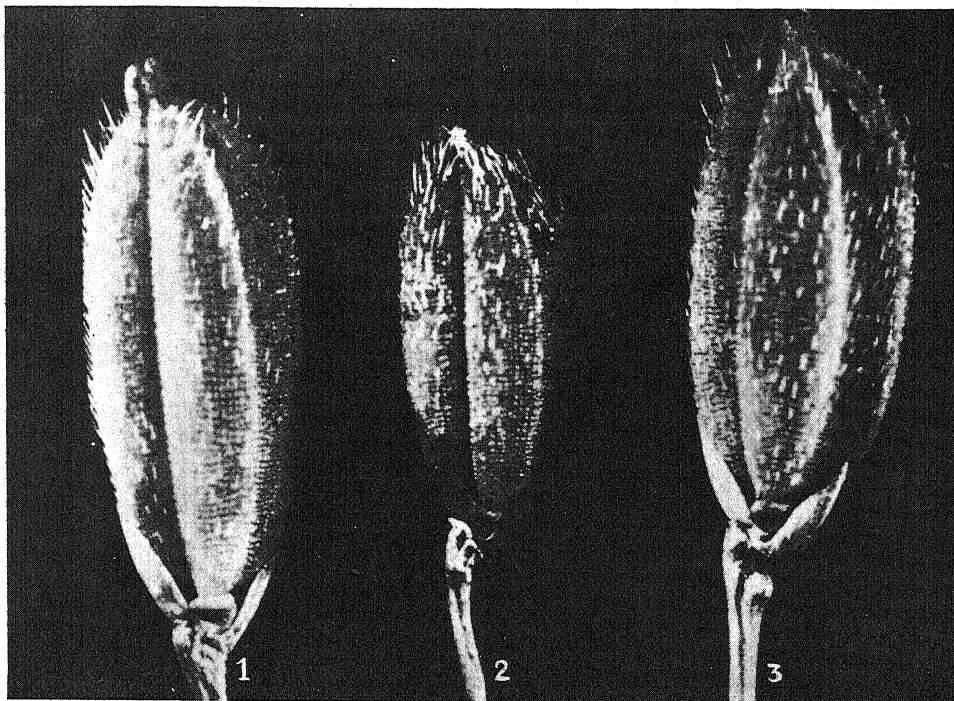


FIG. 98. Spikelets showing the annular enlargement or facet at the apex of the pedicel. 1, Ciliate type ; 2, membranous type ; 3, cup-like (ordinary) type. These " facets " have been interpreted by Arber as the true glumes. (See Fig. 103.) (After Graham.)

Each panicle shows a main axis, the rachis, usually slightly angular, glabrous to ciliate, especially at the nodes, and either erect, half-curved, drooping or sharply curved. This rachis bears a variable number of primary branches, one to several at a node, which form a variable angle with the rachis. As a consequence the panicle may vary from close and compact to loose and spreading. Small secondary branches are in turn carried by the primaries, and on the ends of these branches the spikelets are normally borne.

The length of the main axis and its branches is very varied, and in the same strain is influenced very markedly by environmental conditions. According to Hector (1934) the length of the ear-head in Bengal varieties varies from 16.6 to 28.0 cm. in highland rices and from 14.0 to 42.0 cm. in transplanted Aman rices. In general, the length of the ear-head is correlated with the number of branches. A long panicle tends to have fewer branches.

**THE SPIKELET.**—In a majority of varieties the spikelets are borne singly on the ends of the branches, but in a few varieties they are found in clusters of 2 to 7, presenting an interrupted appearance known as “clustered”. The number of spikelets on a panicle may vary from 50 to 500, though an approximate mean can be detected in a pure line.

Each spikelet is carried on a short pedicel, and is normally 1-flowered, though exceptional 2-flowered types have been reported.

The apex of the pedicel—the facet—is enlarged annularly with the two sides distinctly oblique. Below this enlargement the pedicel is bent or contorted. In many rices the margin of the facet is expanded and thus presents a flanged appearance; in others the facet is cup-like with the rim somewhat thickened; a third type exhibits short hairs on the facet margin (Graham, 1913).



FIG. 99. Variation in length of glumes (? sterile lemmas).

1. Long or winged. 2. Medium. 3. Short. (After Hector *et al.*)

The suggestion was put forward by Cook and by Stapf (1918) that the membranous flanges of the facet might represent the glumes of the spikelet, a conclusion now supported by Arber (1935) and outlined below.

In the great majority of cultivated types the articulation of the spikelet to the pedicel is completely solidified, and the spikelet on being threshed is broken off by fracture. In a few cultivated rices the solidification is not so complete; in many so-called wild rices, partial or complete articulation is found, and the mature spikelets readily fall (Takenouchi, 1924; Bhalerao, 1930).

Above the facet 2 glumes occur, an outer and an inner (see, however, Arber's interpretation below). These glumes are generally small and lanceolate, coriaceous and shiny, approximately equal in length and normally not exceeding a quarter of the length of the lemma. In some rices, however, the glumes may be more than half the length of the lemma or approximately equal thereto. Such varieties are said to be winged. (Fig. 99.) The glumes may be coloured or colourless. When coloured the colour is correlated with colour in the leaf sheath, but the converse

need not be true (Hector, 1913). The colour varies from nearly white to pale yellow to red and black. It may develop early or late, but tends to fade with maturity.

Above the insertion of the glumes, the rachilla expands into an annular thickening. Graham (1913) distinguished two types:—the “comma type”, where the rachilla expands below the insertion of the lemma and then contracts to a slender slightly bent stalk; and the “elbow type”, where the expansion is but slight and the stalk shows but little contraction. (Fig. 100.) Above the thickening the rachilla is very short and slender.

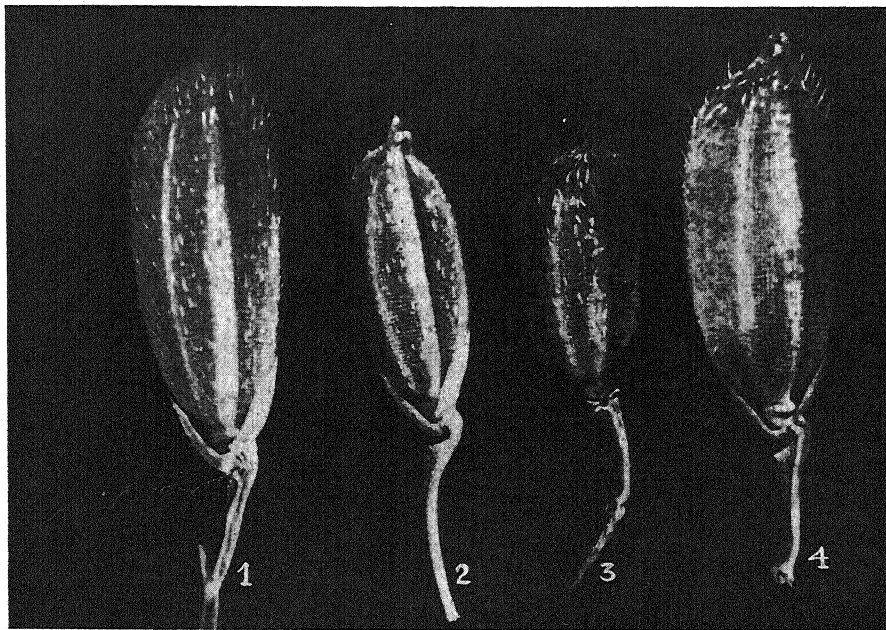


FIG. 100. Variation in Shape of Rachilla.

1. Flat comma type. 2 and 3. Elbow type. 4. Comma type. (After Graham.)

Each flower is subtended by a large conspicuous bract, the lemma. It is approximately boat-shaped, strongly 5-nerved and spinescently hairy on the nerves. The apex is solid and pointed or prolonged into an awn. At either side of the apex or awn, the 2 lateral nerves may project slightly as very short tooth-like projections. Very frequently, pigment develops on the lemma (and also on the palea) independently of that on the glumes, and when present appears to be correlated with colour in the leaf sheath. The converse, however, need not be true. The colour develops gradually and is conspicuous when the husks are mature and indurated. It also exhibits more variation in expression than that of any other part of the plant, but in any one variety is remarkably constant. As a result, colour in the lemma (and palea) has been used in many recent classifications. Unfortunately the colours are somewhat difficult to define. Hector *et al.* (1934) in his classification of the Bengal rices distinguishes five colour classes:—(1) Yellow



—ranging from pale yellow to golden yellow ; (2) Red—ranging from light red to deep red, through buff, orange, brown, etc. ; (3) Black—light black through various shades of grey and purple to deep black ; (4) Piebald red and (5) Mottled. In the piebald types, the shade of red present is found either at the top with the base yellow, or the red is confined to the middle of the lemma with the yellow on the upper and lower portions. In mottled types the colour is more or less confined to the furrows, the ridges being either colourless or faintly pigmented. The colour scheme used by Kashi Ram and Chetty (1934) differs somewhat from that of Hector, viz. : (1) Straw ; (2) Gold, including tip and base gold and piebald



FIG. 101. Spikelet shape.

1, Lemma slightly convex or straight, palea convex ; 2, Lemma slightly convex, palea convex ; 3, Lemma and palea very convex ; 4, Lemma and palea convex. (After Graham.)

gold ; (3) Olive, including piebald olive ; (4) Brown ; (5) Purple ; (6) Ripening black. The same authors also point out that the colour passes through a regular series of stages and in some cases, though the final colour may be the same, the developmental sequence may differ. Thus in purple forms, three types are distinguishable : (1) those in which the purple appears before flowering ; (2) those in which the purple appears after flowering ; (3) those in which the purple appears late in maturity. The inheritance of the colour of the ripe husk is still obscure. Gold and olive have been shown to be recessive to straw, and according to Parnell (1917, 1922) and Hector (1922) appear to be due to the action of several inhibitory

factors. On the other hand, brown, purple and black are dominant to straw-colour, and one, two or more factors may be operative (Parnell, 1917, 1922 ; Nagai, 1921 ; Illife, 1927-28).

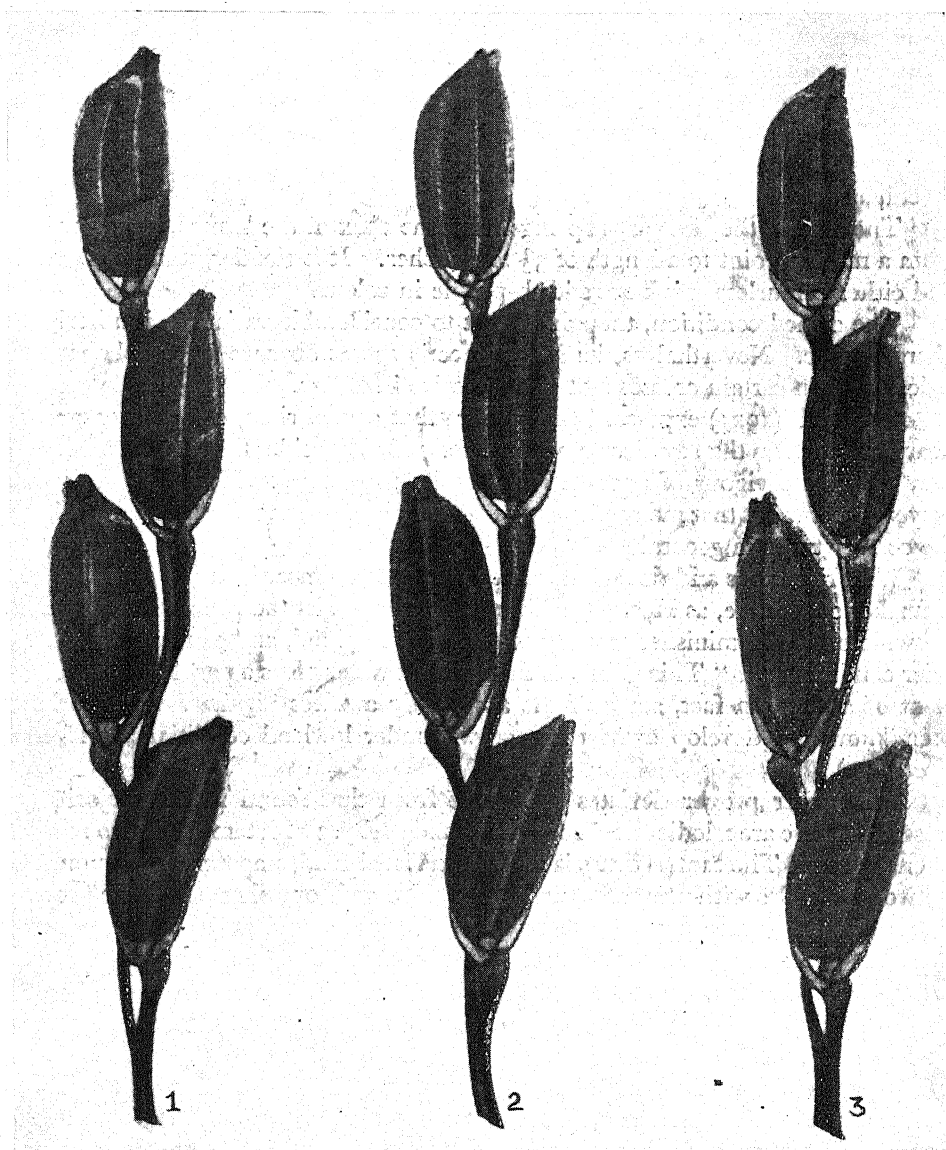


FIG. 102. Four spikelets of three varieties of rice showing exceptional lemma coloration.

1. "Piebald gold," where the "gold" is confined to the upper third of the lemma.
2. "Piebald dark furrow," practically no "gold" showing.
3. "Tipped gold," with no "gold" on the apex. (After Graham.—Original in colour.)



The palea, situated opposite the lemma, is similar to it in shape and texture, but possesses only 3 nerves. The end projects as a short solid point, which together with the apex of the lemma, constitutes the apiculus. In the majority of rices this apiculus has the same colour as the husks. Differential pigment, however, may be present, and varies from vermilion to deep purple. In many cases it develops very early and may persist to maturity. In other types the colour is transient and is almost indistinguishable at maturity. Hector (l.c.) showed that all varieties which have colour in the apiculus have also colour in the leaf sheath and the glumes, but that the converse of this correlation is not always true. One, two or more factors, giving 3 : 1, 9 : 7 ; 27 : 37 and 15 : 1 ratios, may be concerned in apiculus colour.

The awn in the rice plant springs from the apex of the lemma, and may vary from a minute point to a length of  $3\frac{1}{2}$  to 4 inches. It is slender, minutely scabrid and either colourless, pink or reddish-purple in colour.

The awned condition, though subject to considerable variation, is a heritable characteristic. Nevertheless, its inheritance is as yet obscure since it behaves as a dominant in certain crosses and as a recessive in others.

Copeland (1924) expressed the opinion that awned rices, on the average, are heavier producers than awnless types, and seemed to consider that this is so because they retain the vigour of ancestral wild and awned types. Hector *et al.* (1933), however, point out that many of the high yielding Bengal types are awnless although the coarser types in general are awned.

Wild rice types and deep-water rices are indeed almost invariably awned. It is further suggestive, as Hector (l.c.) has pointed out, that the proportion of awned to awnless types diminishes as one passes towards upland, and generally speaking, drier conditions. "This points to the fact that water plays a part in the development of awns. In fact, some of the apparently awnless highland varieties have been known to develop awns when grown under lowland conditions" (Hector *et al.*, l.c.).

The flower proper deviates somewhat from that found in the majority of grasses. There are 2 lodicules, broad, thick and fleshy. Six stamens in two regular whorls follow. The central ovary is longer than it is broad, smooth and surmounted by two long styles with plumose stigmas. A third style or a short stigmatic process may be present. The colour of the style is either white or coloured pink to purple. It would appear that when the stigma is coloured the leaf sheath is always coloured, but that the converse is not necessarily the case.

In the above description, the spikelet has been described as possessing 2 glumes and having a single fertile flower subtended by a lemma and a palea. This is the usual interpretation. Another interpretation, however, has been indicated above, viz., that the two membranous margins of the facet are the true glumes. In support of this concept Arber has recently shown that these membranes are vascular. On this interpretation the spikelet would have 3 lemmas, the first and second (corresponding to the first and second glume of the usual interpretation) being infertile, the third (corresponding to the single lemma of the usual interpretation) being fertile. Such an interpretation would also bring the structure of *Oryza* into line with that found in certain species of related genera.

ANTHESIS, POLLINATION AND FERTILIZATION:—The period

at which rice commences to flower varies with the variety and the environmental conditions. It is generally spoken of as the "time of flowering". The period from the date of sowing to the "time of flowering" has been termed the "flowering

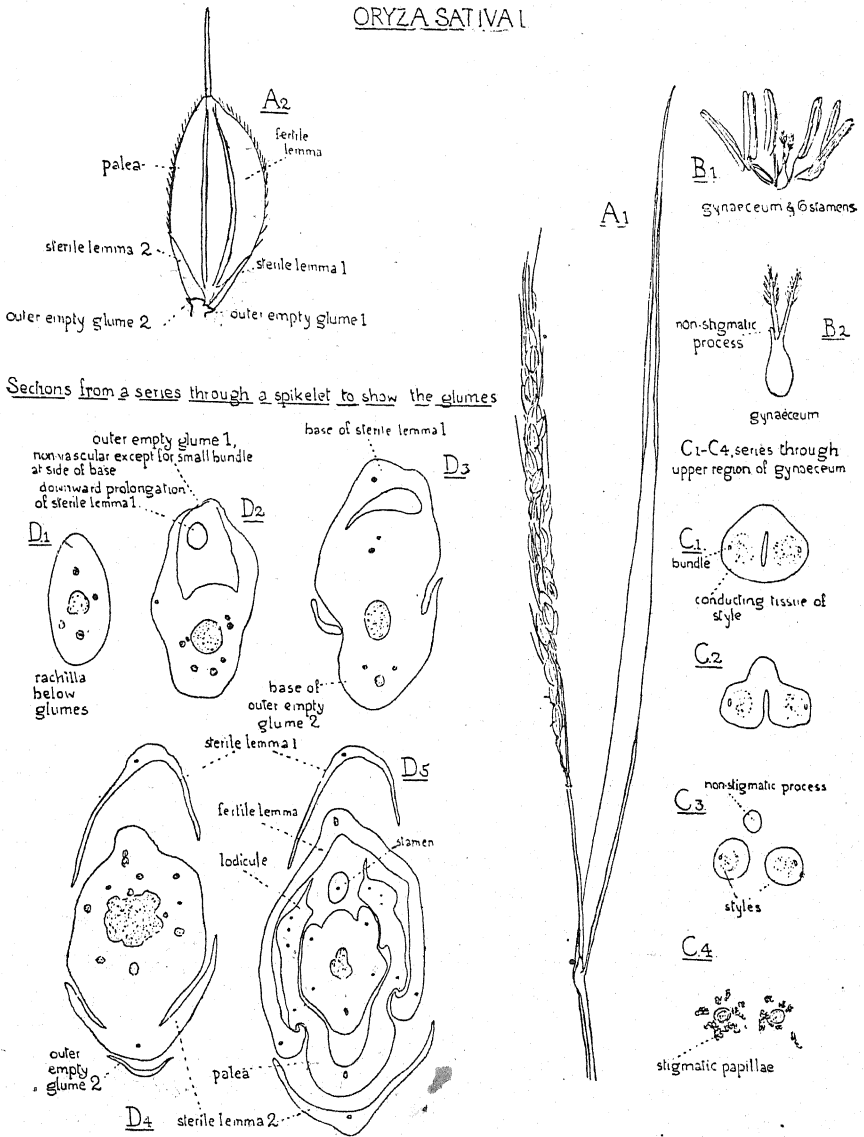


FIG. 103.

*Oryza sativa* L. A 1, Inflorescence, Cambridge Botanic Garden ( $\times \frac{1}{2}$ ). A 2, Spikelet ( $\times 3$  circa). B 1, Gynaecium and 6 stamens. B 2, Gynaecium more enlarged. C 1—C 4, Series of transverse sections from the base of the styles upwards ( $\times 47$ ). D 1—D 5, Sections from a transverse series from below upwards ( $\times 47$ ) through a young spikelet to show the succession of glumes. (After Arber, *The Gramineae*, by permission of the Cambridge University Press.)

duration". In India it may range from 60 to 180 days and is influenced by such factors as spacing, the food supply and particularly by the time of sowing.

The reaction to time of sowing, however, depends on the nature of the variety. Some varieties, *e.g.*, the "Aus" types of Bengal, are "periodically fixed". In these forms the earlier they are sown, the earlier is the onset of flowering; the later they are sown, the later the flowering; but in each instance, within limits, the duration remains practically constant for the variety in question. The "period" is fixed. On the other hand many late varieties and the transplanted winter varieties of Bengal, are "timely fixed". The actual date of flowering is so constant that no matter when the variety is sown and transplanted, it comes into flower at approximately the same date every year. The "time" is fixed (Mitra, 1932).

The inheritance of flowering duration has been studied genetically by several investigators (van der Stok, 1910; Hoshino, 1915; Nomura and Yamasaki, 1925; Bhide, 1926; Jones, 1928; Ramiah, 1933). Ramiah (*l.c.*) found that in some instances there was only a single factor difference between earliness and lateness; in other cases, the situation was complex and could only be explained by a multiple-factor hypothesis. "When the number of factors involved is great, the  $F_1$  appears to be intermediate between the parents and in  $F_2$  we either get a transgressive variation or a variation within the parental limits and the parental types are hardly recovered. Varieties that have the same flowering duration may still differ in their factorial composition with regard to this character, giving a transgressive variation in the  $F_2$  when crosses are made between them."

Also, as already noted, Ramiah (1933 b) established a definite correlation between plant height and flowering duration, which appeared to be positive in early varieties and negative in late varieties.

Anthesis commences on a panicle shortly after it emerges. The first spikelet to open is generally the terminal one of the main axis followed thereafter by those of the main branches. On the whole anthesis proceeds from above downwards. A single panicle completes its flowering in 6 to 9 days. According to Sethi and Saxena (1930), early varieties in the United Provinces, India, attain their maximum flowering during the second and third day of the flowering period and finish by the sixth day, whilst late varieties only reach their maximum on the third and fourth day and may continue flowering up to the seventh and even the ninth day.

According to Hector (1913) the individual spikelet in the case of the early varieties of Bengal usually commences to open about 10 a.m.; in the case of the late Aman varieties, flower opening does not begin until between 9 and 10 a.m., and may continue until midday. Other observers in India are more or less in agreement (Thompstone, 1915; Bhide, 1925; Rao, 1926; Ramiah, 1927; Bhide and Bhalerao, 1927; Kadam and Patel, 1933, etc.). Weather conditions, and especially temperature, however, have a marked influence. There seems to be little or no flowering below  $77^{\circ}$  to  $78^{\circ}$  F. (Ramiah, 1927). In the Philippine Islands, Tores (1923) and Rodrigo (1925) reported that anthesis occurs between 9 a.m. and 11.30 a.m., whilst in Texas, Lande and Stensel (1927) found blooming from 8 a.m. to 4 p.m., the peak occurring between 11 a.m. and 12 noon.

The opening of an individual flower is rapid, and is probably due to simultaneous swelling of the lodicules and lengthening of the filaments.

The bracts move apart at first somewhat slowly, but towards the end much more rapidly. When fully extended they make an angle of  $30^{\circ}$  to  $35^{\circ}$  with one another. The whole movement is complete in about 10 minutes. Simultaneously with the falling apart of the bracts the anthers emerge and in a few seconds are pendant. Dehiscence of the anthers may take place just prior to the opening, at the moment of emergence or after the anthers have fully emerged. In most cases, however, dehiscence takes place—almost explosively in certain instances—at the moment of emergence. The stigmas become visible as the anthers become pendant, and are then generally found to be already dusted with pollen. The period during which a flower remains open is very variable, and ranges from about 30 to 90 minutes (Hector, 1913).

Since rice pollen is normally shed either just before the flower opens or at the moment of flower opening, self-pollination followed by self-fertilization is the rule. Nevertheless, a variable amount of cross-fertilization may take place. This varies with the variety and locality. Thus Hector (1913) found that under favourable conditions in Bengal cross-fertilization could take place to an extent of about 4 per cent. Akemine and Nakamura (1924) found a racial difference which varied from 0.21 per cent. in Kuromochi rice to 2.32 per cent. in Sasaki. Stride (1923) classified rice into three groups having respectively open pollination, variable pollination dependent on climatic conditions and closed pollination. In Java, however, the percentage found has reached the high figure of 25 per cent.

The pollen of glutinous rice (see page 295) differs physiologically from that of non-glutinous. On treatment with iodine, glutinous rice pollen gives a red reaction, indicating the presence of amylo-dextrin. The non-glutinous condition has been shown to be dominant (or partially dominant) to the glutinous conditions. (Moquette, 1905; van der Stok, 1910; Parnell *et al.* 1921.) In many cases, however, there occurs a definite departure from the expected ratio of 3 starchy to 1 glutinous. Parnell (*l.c.*) by micro-chemical tests found that the two types of pollen grains were present in a hybrid in the expected ratios. As a consequence he invoked a differential germination of the two pollen types to explain the deficiencies met with. Chao (1928) postulated a differential growth type. These explanations parallel those adopted to explain deficiency of waxy maize, in the cross waxy and non-waxy. In the case of rice, however, the phenomenon has not yet been studied in sufficient detail.

**STERILITY.**—Sterility is wellnigh universal in rice. It may vary from the presence of a few empty spikelets to an almost complete sterility of the whole panicle.

When occasional empty spikelets occur the sterility is generally due to lack of fertilization. This may be the result of unfavourable weather conditions or to anther degeneration. If due to anther degeneration it may be an inherited condition. Often a smaller or larger portion of the top of the panicle may exhibit rudimentary spikelets which are white and papery in appearance, tending to dry up and break down shortly after they emerge. This condition—known as “sponginess” in Java—may be due to environmental conditions, but in most cases appears to be due to abortion of both the anthers and the ovaries. According to Bhide and Bhalerao (1927), “sponginess” in Kolomba rice is generally associated with types having short compact panicles and short fine grain.

If the sterility affects the whole panicle it may be due to stalk-borers, eel worm, fungus infection, physiological conditions or be a heritable condition.

In many instances, sterility is known to have arisen as a mutation, and the progeny (when obtainable) have given abnormal segregation ratios. Various explanations have been advanced. Terao (1917 and 1921) expressed the opinion that a change from a dominant fertile condition to a recessive sterile or semi-sterile condition may take place in the somatic cells, and assumed a sex-linked lethal factor in one instance. Nagai (1927) studied both sterile and semi-sterile mutants but found no satisfactory explanation. Ishikawa (1927) classified the forms studied by him into sterile, semi-sterile and partially sterile types. In sterile forms, abortive pollen was found; in semi-steriles, embryoless ovules occurred; in partially-sterile, the reproductive organs appeared normal, and a lethal factor was again assumed to account for the segregations obtained. Other investigators (Bhide, 1922; Suzuta and Suematu, 1927; Nakamura, 1931, Miyazawa, 1932; Isshiki, 1933; Miyazawa, 1935; Ramanujam, 1935, etc.), have noted that anther or ovule degeneration, or both, may occur. Both simple and complex segregation in these instances were found. No satisfactory genetical explanation of the phenomenon has as yet been advanced, and detailed cytological studies have not so far been carried out.

The development of the gametes is similar to that of other cereals (Terada, 1927-28; Noguchi, 1929; Kuwada, 1910). The first of these authors also found two embryo-sacs in one ovule. Rodrigo (1925); Jones (1928); Komuro (1932) and Ramiah *et al.* (1935) have described instances of poly-embryony. Ramiah *et al.* (l.c.) found it to be a common phenomenon in one pure line (T.24 at Coimbatore), occurring in the preparation of 1 in 1,000 seeds. Although grains giving rise to 2 seedlings were the commoner, occasional triplets were produced. Both genetically identical and genetically different twins occurred. In the instances where genetically different twins were produced (*e.g.*, the green-albino twin) Ramiah *et al.* point out that such types could only be formed from the development of 2 embryo-sacs.

**THE MATURE GRAIN.**—The grain of rice at maturity is enclosed in the lemma and palea. The husk so formed may firmly enclose the grain or the grain may be more or less loose within the husk. The colour of the mature indurated husk has already been dealt with.

The colour, shape and size of the kernel or caryopsis vary. Colour in the caryopsis is located in the pericarp and is readily removed in the milling process, except in the case of varieties with ridged kernels where some of the colour may adhere to the surface of the de-corticated grains. Hector (1934) found that the Bengal rices varied in colour from white to charred black. Three common groups were recognized:—White (dull to glossy white), amber (including the lighter shades of red), and red (including the deeper red shades such as vermilion, terracotta, etc.). Three exceptional forms also occurred, sprinkled or mottled (where some red pigment is sprinkled on the surface); piebald (where there is a deeper shade of colour on the margins and a lighter shade in the centre) and charred black (where there is very deep colour due to the presence of red and purple pigments, with the embryo regions lighter in colour than the rest of the grain).

The shape of the caryopsis is in the main determined by the shape of the

lemma and palea. Graham (1913) recognized five groups of husked grain :—those with (1) lemma and palea slightly convex ; (2) lemma and palea convex ; (3) lemma and palea very convex ; (4) lemma slightly convex, palea convex, and (5) lemma slightly convex or straight, palea straight or slightly concave. Four sizes of hulled grain were distinguished :—(1) long spikelets in which the length is more than four times the breadth ; (2) fine, in which the length is more than three times the breadth ; (3) coarse, in which the length is more than twice the breadth and (4)



FIG. 104. Polyembryony in rice seedlings.

- a. A seed with 2 seedlings.
- b. A seed with 3 seedlings. (After Ramiah et al.)

round, in which the length is less than twice the breadth. In more recent classifications, measurements of the de-hulled grain have been employed, the length, breadth and thickness being taken into consideration. The  $\frac{\text{length}}{\text{breadth}}$  index,  $\frac{L}{B}$ , and also the  $\frac{\text{length}}{\text{breadth} \times \text{thickness}}$  index,  $\frac{L}{B \times T}$ , have also proved useful criteria. Thus, Hector (1934) in his classification of Bengal rices differentiates two groups : (1) the oval-grained, when the length is three times or less than three times the breadth ; and (2) oblong-grained, when the length is more than three times the breadth. Each of these can then be subdivided into fine, medium and coarse, the differentiation being based on length and  $\frac{L}{B \times T}$  index.

Chao (1928) found that short spikelet was dominant to long. Ramiah *et al.* (1931) showed that the short round was dominant to long narrow. It was further surmised that the factor or factors responsible for spikelet length might be different from but closely associated with those for shape. In a further study, Ramiah and Partha-sarathi (1933), showed that there is a positive correlation between length and the  $\frac{L}{B}$  index, indicating that long grains tend to be narrow and short grains broader than long ones. Inheritance studies showed that both length and width were due to multiple factors, both inter-related.

The surface of the caryopsis exhibits longitudinal grooves and ridges, which vary very considerably in their expression. Both base and apex are blunt and the embryo is situated at the base of the dorsal side. About the middle of the dorsal side, a chalky white spot may be present—the so-called “abdominal white” of Kikkawa.

**STRUCTURE OF THE GRAIN.**—**HUSK.**—(Lemma and Palea).—Here the structure is very characteristic. The cells of the outer epidermis are large, more or less square in outline, with thick, strongly sinuous walls, and arranged in parallel longitudinal rows. Stiff dagger-like hairs—up to 800mm. long and 40mm. wide—are abundant. Below the epidermis two to three layers of elongated sclerenchymatous fibres occur. This is succeeded by a mesophyll of rectangular cells with thin wavy walls. The inner epidermis is much compressed, and consists of elongated and cubical cells with thin striated walls.

**PERICARP.**—1. *Epidermis* (Epicarp).—The cells are transversely elongated (120 to 500  $\mu$  long by 30 to 100  $\mu$  wide) with the end walls waved in a peculiar manner not seen in any other cereal.

2. *Mesocarp*.—Several layers of highly compressed elongated cells with comparatively thin walls.

3. *Cross-cells*.—A single layer of loosely arranged and much elongated cells, generally straight but sometimes bent and even branched. They may reach a length of 500  $\mu$  but are only 4 to 6  $\mu$  wide.

4. *Inner Epidermis* (Tube cells).—Here the cells are separated from one another, and arranged at right angles to the cross-cells, which they closely resemble, though narrower.

**TESTA.**—A thin practically structureless layer, the remnant of the inner integument.

**NUCELLUS.**—The nucellar epidermis may be distinguished after treatment with potash and chlorzinc iodine as a single layer of elongated cells with reticulate radial walls.

**ENDOSPERM.**—The endosperm consists of a single layer of polygonal aleurone cells, with a central mass of thin-walled starch parenchyma.

Two types of endosperm are known—the non-glutinous or translucent and the glutinous. In non-glutinous rice, the endosperm is hard, brittle and translucent. The cells contain numerous small starch granules, often compounded into oval aggregates of several hundred grains. On account of their hard texture, they are less easily damaged during transportation and mill better than the glutinous rices, whilst the kernels after a period of storage show practically no tendency to stick together on cooking.

The endosperm of glutinous rices is comparatively soft and opaque, more or less chalky in texture. On treatment with iodine it gives a red coloration, due to the presence of dextrine. Glutinous rice—even after storage—tends to form a sticky mass when cooked. About the middle of the dorsal side of the endosperm, many varieties exhibit a crescent-shaped area where the starch grains are loosely formed and mixed with dextrine. This condition was termed “abdominal white” by Kikkawa. It may be due to immaturity and was regarded as such by Graham (1913). Hector (1934), however, states that there is a genuine “abdominal white”, which is not due merely to immaturity, and is both heritable and fairly constant in its expression. It occurs in both non-glutinous and glutinous varieties. In glutinous rice, the condition tends to be masked by the rest of the endosperm and is not readily detectable. In non-glutinous rice the chalky abdominal area may be very prominent.

The non-glutinous condition has been found to be dominant over the glutinous and abdominal white conditions, and exhibits mono-factorial segregation. (See also page 291.)

**EMBRYO.**—The embryo of rice exhibits no unusual features, possessing in addition to the normal structures a distinct epiblast.

**GERMINATION AND THE SEEDLING.**—Rice is said to have no dormant period and can germinate at any time after it is completely mature. It loses its vitality slowly under suitable conditions of storage. Copeland (1924) states that under Californian conditions the loss in vitality is less than 10 per cent. per annum, whilst in the Philippines it may be 15 per cent. per annum.

Akemeine (1914) found the minimum temperature for germination to be 10° to 13° C., the optimum 30° to 35°, the maximum 40°. Other investigators have obtained more or less similar figures, but it would appear that varieties grown under the more temperate conditions are those which can germinate at lower temperatures than the tropical varieties.

Akemeine (l.c.) also found that the grains absorb water to the extent of about 25 per cent. of their air-dry weight, giving a total water content of approximately 35 to 40 per cent. at germination. Submersion in water does not inhibit germination but in moist soil the germination is more rapid. Direct experiment has also shown that non-inhibition of germination by submersion in water is due to the low oxygen requirement of the grain. Peirce (quoted by Copeland) found that the heat liberated during germination is much lower in rice than in other seeds.



Under optimum conditions, the first indication of germination is detectable after about two days. In the field it varies with the water content and the temperature. On moist soil the radicle appears first and the shoot thereafter; subsequent growth of the shoot is also slow. On the other hand, when the grains are submerged, the coleoptile appears first and the appearance and subsequent growth of the radicle is delayed.

The seedling develops 1 primary root, a so-called "mesocotyl" of variable length and a shoot at first enclosed in the coleoptile.

**CYTO-GENETICS AND BREEDING.**—The first genetical studies on rice were those of van der Stok (1910), followed by the work of Hector and Parnell in India. Subsequently, much work has been done both in India, Japan and California. This work up to 1927 has been reviewed by Ikeno. Mono-factorial segregation of many characters has been demonstrated, but at the same time even the same character in different crosses may exhibit complex ratios. Some of the more important of these ratios have been discussed in the text.

Evidence of linkage in the above investigations has been obtained, and Yamaguti (1926, 1927, 1929) has identified four linkage groups, and Chao (1928) three and possibly four. As the chromosomes are twelve in number, much work remains to be done.

Kuwada (1910) found that the haploid chromosome number is 12, since confirmed by Nakatomi (1923), Rau (1929) and others. Nakatomi (1923) also claimed that there was a varietal difference in the size of the chromosomes.\*

Kato *et al.* (1930) distinguished two types of rice, var. *japonica*, indigenous to Japan and Korea, and var. *indica*, indigenous to Southern China, India and Java. Varieties of *japonica* and of *indica* are mutually inter-fertile, but hybrids between the two types are less fertile and exhibit varying degrees of pollen degeneration. Jones (1930) also found marked sterility between hybrids of the Japanese and Chinese varieties. Selim (1930) studied five varieties, of which one definitely belonged to *japonica* and two to *indica*. All five possessed the same nuclear size and chromosome number. They differed, however, in the nucleolar content of the pollen and megaspore mother cells. The two *indica* varieties (and an unnamed Egyptian variety) exhibited two permanently attached nucleoli during prophase; the *japonica* variety (and the Egyptian variety Nabatat 1) had only one such nucleolus.

Recently the occurrence of haploid types has been reported (Morinaga and Fukushima, 1931; Nakamura, 1933; Ramiah *et al.*, 1934). All the haploids are dwarf and markedly sterile. They frequently exhibit partheno-carpy and very occasionally may be self-fertilized or fertilized by a diploid to give homozygous normals. Further, some of the tillers produced by a haploid may be diploid. At meiosis there are 12 unpaired chromosomes which are distributed at random to the poles. (Morinaga and Fukushima, 1932.) In a later report (1934) the same observers found occasional bivalents.

\* Recently Sethi (Sethi, B.L., 1936, "Cytological Studies in Paddy Varieties," J. Ind. Agr., Sci. 7: 687-703) has studied a number of Indian varieties. Despite diversity of type and geographical distribution, all varieties possessed 12 (n) and 24 (2n) chromosomes. The complements of different types, however, showed definite variation in morphology. At meiosis variability in behaviour also occurred, and a positive correlation was found to exist between meiotic irregularity and sterility. Sethi concludes that *Oryza Sativa* can be regarded as a Secondary polyploid which originated through the natural fertilization of species in related sub-families of the Oryzeae, possessing five and seven chromosomes.

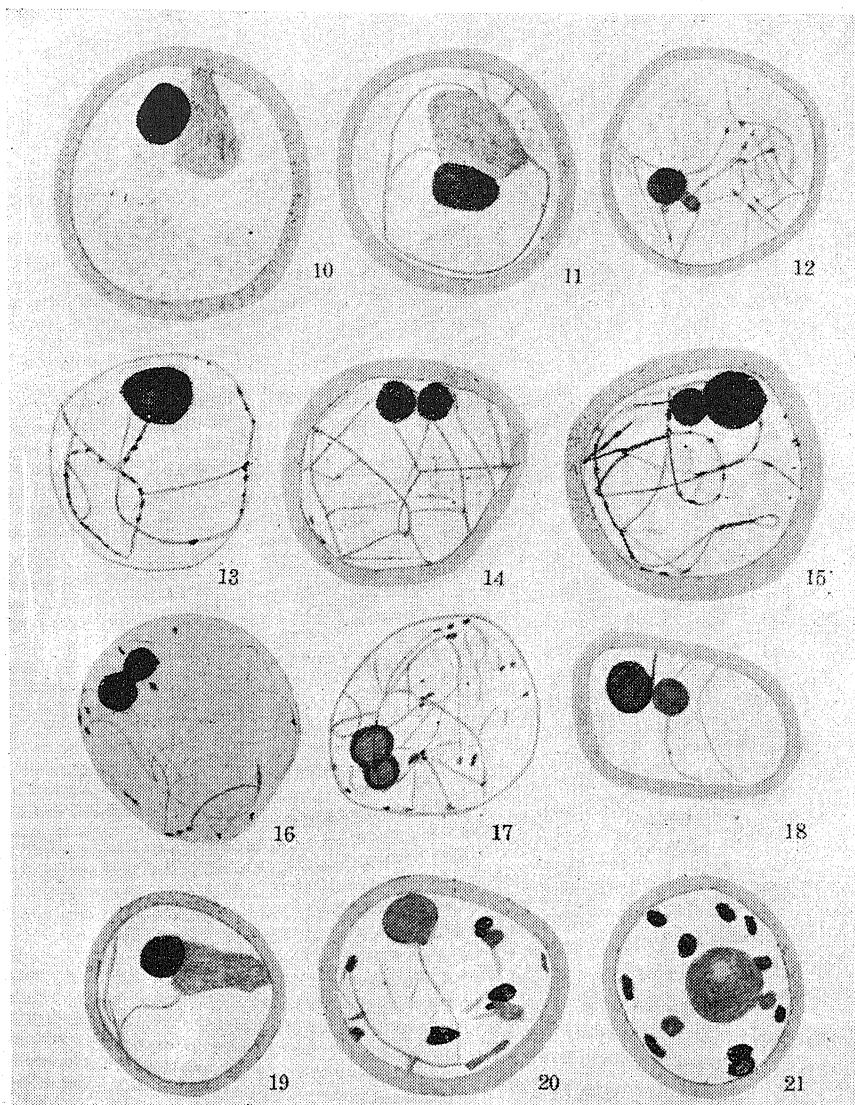


FIG. 105.

10 to 20, pollen and megaspore mother-cells — X ca. 2160; 21, pollen mother-cell, X ca. 2880.

- 10, "New Japanese 6," synizesis with single nucleolus; 11, "Nabatat 1," synizesis with single nucleolus; 12, "Temas," megaspore mother-cell, loosening synizetic knot with a large and a small nucleolus; 13, "Nabatat 1," synapsis with single nucleolus; 14 and 16, "Kochivittu," reticulate spireme attached to two equal nucleoli; 15, "Unnamed Egyptian" race, reticulate spireme attached to two unequal nucleoli; 17, "Kochivittu," megaspore mother-cell, reticulate spireme and two nearly equal nucleoli; 18, "Kochivittu," megaspore mother-cell, unequal nucleoli with the secondary nucleolus staining paler; 19, "New Japanese 6" megaspore mother-cell, synizesis with single nucleolus; 20, "Unnamed Egyptian" race, development of the chromosomes; 21, "Kochivittu," diakinesis with one pair of chromosomes attached to the nucleolus. (After Selim.)

Triploid plants of unknown origin have also been found (Nakamura, 1932; Morinaga and Fukushima, 1935). They are distinguished by their greater vigour from normal plants but are markedly sterile. At meiosis, 12 configurations, presumably trivalents, were found in the pollen mother cells, though occasionally more than twelve were seen. An irregular plate formed at metaphase and at anaphase the trivalents disjoined two to one. Occasionally univalents lagged and divided. The second division was fairly regular and tetrads with four cells formed. Few pollen grains, however, matured. In the ovules, meiosis was similar to that in the anthers and very rarely an embryo or endosperm was noted, which may have been due to fertilization.

Nakamori (1933) has reported the spontaneous occurrence of a tetraploid plant. The spikelets produced were larger than in the triploids but the fertility was still further reduced. Ramiah *et al.* (1935) have also reported the occurrence of a tetraploid in the wild rice (*Oryza longistaminata*). The plant throughout was larger than the diploid, even to the extent of possessing longer pollen grains. Meiosis was regular. The number of quadrivalents was 7 to 11, with variable lagging univalents. Secondary association—in groups of threes and fours—was noted and this phenomenon, taken in conjunction with its presence in other forms, appears to indicate that the basic chromosome number in *Oryza* may yet prove to be fewer than 12.

A large number of mutations, many of them defective types, have been observed in rice. Ichijima (1934) succeeded in producing mutations paralleling all the known forms by treatment of pure lines with X-rays, ultra-violet rays and temperature change. In addition, 2 of the plants obtained were heteroploid ( $2n + 1$ ), 6 were triploid ( $3n = 36$ ) and 1 tetraploid ( $4n = 48$ ). The behaviour of these polyploids at meiosis was more or less similar to that of the spontaneous forms discussed above.

**CLASSIFICATION AND ORIGIN OF CULTIVATED RICE.**—The genus *Oryza* includes some eighteen to twenty species reviewed recently by Roschevitz (1931) and Chevalier (1932). The section *Sativa* is the most widely spread, including twelve species. Of these species, *O. sativa* var. *spontanea* approximates very closely to the cultivated varieties, and has an area of distribution in India and Indo-China which coincides with the areas of most ancient cultivation. This species may be regarded as the progenitor of the majority of cultivated races. Other species, however, may have played a part. Thus, certain of the small-grained rices may have arisen from *Oryza minuta* Prest. (Koernecke). According to Chevalier and Roehrich (1914) some of the West African rices may be derived from *O. breviligulata* Cheval et Roehr. Watt (1891) also regarded *O. officinalis* as related to several of the Asiatic types.

Although *O. sativa* f. *spontanea* has its centre of diversity in India and Indo-China, the centre of origin of the section *Sativa* as a whole must be regarded as Africa, where seven of the twelve species occur. It is therefore possible that the primeval home of rice may be tropical Africa, but if that be the case, then its introduction into Asia must have taken place at a very early date.

In the East, rice is known to have been in cultivation for several thousand years; its prehistorical period of cultivation or semi-cultivation may, therefore, run into many thousands of years. During the whole of this period it has been

intensively grown by peasant farmers, under conditions favourable to the development of local races. Further, rice is mainly self-fertilized. As a consequence rice is now a vast complex of forms, whose extent it is scarcely possible to gauge. According to Copeland, in Java, Indo-China and Japan, the number of varieties is estimated at approximately 1,000 each. In the Philippines, some 3,500 varietal names are on record, and up to 1919 nearly 1,000 of these had been proved to be distinct. In Ceylon, the estimate is only 200. Even an approximate estimate for China is not available. In India, 8,000 varietal names are said to have been recorded. How many of these are distinct it is as yet impossible to say. Hector *et al.* (1934) have described 856 types of transplant *aman* and 931 types of highland *aus*, classifiable into 540 varieties, for Bengal alone! There are, however, over 20,000,000 acres under rice in Bengal! Elsewhere in India the numbers must also be high. Thus, Ram and Chetty (1934) have already described 123 types from Bihar and Orissa, and Sethi and Saxena (1930), 135 types from the United Provinces.

In view of the amount and complexity of the material, the classifications at present in use can only be regarded as provisional. In India the first classifications were purely morphological and based on insufficient material (Roxburgh, 1874; Duthie and Fuller, 1882; Watt, 1891; Hooker, 1897; Gammie, 1908). In 1912, Kikkawa grouped the rices of Burma by means of the characters of the grain. Graham (1913) published a preliminary classification of the rices of the Central Provinces. Beale (1927) outlined a classification for Burmese rice whilst Thadani and Dutt (1928)—on the primary basis of awning—classified some of the rices of Sind. Bhide and Bhalerao (1927) studied the types of Kolamba rice of the Bombay Presidency. Sethi and Saxena (1930) dealt with the rices of the United Provinces. The rices of Bihar and Orissa have been studied by Kashi Ram and Sarvayya Chetty (1934). The most comprehensive analysis, however, is that of the Bengal rices by Hector and Sharngapani (1934).

These investigators first divide the varieties into five groups:—the translucent rices, the glutinous rices, the winged rices, the clustered rices and the double-grained rices. Further subdivision is then based on:—1. Distribution of colour or absence of colour in the vegetative parts. 2. Presence or absence of awns. 3. Colour of the ripe husk. 4. Colour of husked grains. 5. Consistency of grain. 6. Shape and size of grain (oval fine, medium coarse, oblong fine, medium coarse, depending on measurements). Types within the varieties are then grouped into highland *aus* and transplant *amans*, according to date of sowing and harvest, and each again into early, medium and late, according to duration from sowing to harvest. In this manner 540 varieties and 1,787 types have been analyzed. Outside of India, analysis of varieties has proceeded on similar though less extensive lines.

The differentiation of rice into the two fundamental forms, *japonica* and *indica* by Kato *et al.* (1930) has already been discussed (page 296).

**PHYSIOLOGICAL STUDIES.**—Until recently but little physiological work—with the exception of the work done on the nitrogen problem—has been carried out.

In 1884, Kellner showed that the rice plant required ammoniacal nitrogen during the early stages of its growth and nitrate nitrogen in the later stages. This

conclusion was confirmed by later workers (Nagoka, 1904; Daikuhura, 1905; Aso and Bahadur, 1906; Krauss, 1907; Kelley, 1911; Trelease and Paulino, 1920; Espino, 1920, and others). As a result of these experiments it was generally accepted that nitrogen in the form of ammonia was the more beneficial, except at the flowering stages, when nitrate nitrogen was also absorbed.

Dastur (1931, 1932, 1933) and Dastur and Malkani (1933) reinvestigated the problem. They found that there was unequal absorption of ammonium and sulphate ions from solutions of ammonium sulphate and from those of all other ammonium salts. The absorption of the ammonium ions decreased as the plant aged, while the absorption of nitrate ions from nitrate solutions, low in the early stages, increased as the plant grew older.

Dastur and Pirzada (1933) then studied the growth rate. They found—with seedlings transplanted in July—that (with all treatments), the relative growth of the whole plant, the relative growth rate of the leaves and the leaf area ratio, reached their maximum in August. The results indicated that the maximum benefit from manuring would be obtained if the fertilizers were applied when the relative growth rate was at its maximum. This was found to be the case. The fresh and dry weights, the leaf areas and the volumes of the roots when manured on the 15th of August with a nitrogenous fertilizer, such as nitrate or ammonium sulphate, or both together on an equal total nitrogen basis, were higher than when the plants were manured at any other period. (Dastur and Pirzada, l.c.) Also, the best results were obtained by using a mixture of ammoniacal nitrogen and nitrate nitrogen at the critical period. The plants so treated also showed a maximum carbohydrate content. They concluded:—1. That a mixture of two forms of nitrogen is a better fertilizer than any one by itself; 2. That the application of the fertilizer should be made early in August or even at the time of transplantation; and 3. That late manuring has very little effect on the growth and yield.

In a later paper Dastur and Kalyami (1934) have attempted an explanation as to why the rice plant should be able to absorb ammoniacal nitrogen in the earlier stages of growth and nitrate nitrogen in the later. By studying the pH of the solutions and the plant tissues, and also the iso-electric point of the rice proteins, they found that during the early stages of growth the pH of the proteins of the protoplasm was on the alkaline side of their iso-electric point and their roots were growing in an alkaline medium. This favoured the absorption of the basic ions, and ammonium ions were consequently absorbed in greater numbers than potassium or sodium ions. The nitrate nitrogen was not absorbed since the nitrate ions are acidic and the proteins combined less readily with the anions than the cations. During the later stages, however, the pH of the proteins passed to the acidic side of their iso-electric point; as a consequence, acidic ions, such as the nitrate ions were more and more absorbed as the plants aged, whilst the absorption of the ammonium ions decreased. "Thus the diffusion of ammonium nitrate ions into the roots of the rice plants depends upon the pH of the proteins of protoplasm. The changes in the pH bring about a preferential absorption of one or the other ion as the case may be."

Recent work has also shown that the rice plant is markedly influenced by length of day (Hara, 1930). By decreasing the period of illumination, the shorter but the more intensive is the growth. Further, the maximum response is obtained

by applications of short light periods during the early stages of the plant's growth. (Noguchi, 1930; Fuke, 1931; Kondo *et al.*, 1932). Kondo *et al.* (l.c.) also kept plants under continuous illumination for three years. No panicles were produced throughout the period. At the end of the experiment, however, the plants when restored to natural conditions, flowered and set grain.

These reactions to the light period must in future be considered in the study of local varieties, especially in connection with their origin.

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## CHAPTER VIII

### MILLETS

THE term "millet" is applied to a number of annual grasses, used both as forage and cereal crops. They belong to several fairly closely allied genera of which the most important are *Echinochloa*, *Setaria* (*Chaetochloa*), *Panicum* and *Pennisetum* of the tribe Paniceae, and *Eleusine* of the tribe Chlorideae.

The following key will serve to differentiate the more common species.

- A. Inflorescence spicate. Involucre of bristles below each spikelet.
- B. Spikes simple.
  - C. Spikes loose, grains enclosed in lemma and palea at maturity . Fox-tail Millet  
(*Setaria italica*, Beauv.)
  - CC. Spikes dense ; grains becoming free of lemma and palea at maturity . . . . . Pearl Millet  
(*Pennisetum typhoides*, Stapf and Hubbard.)
- BB. Spikes more or less digitate . Finger Millet  
(*Eleusine coracana*, Gaertn.)
- AA. Inflorescence paniculate. No involucre below each spikelet.
- B. Inflorescence a drooping panicle. No awns . . . . . Broom-Corn, or Proso-Millet  
(*Panicum miliaceum* L.)
- BB. Inflorescence a raceme of short spikes, awned . . . . . Japanese Barnyard Millet  
(*Echinochloa frumentacea*, Link.)

### FOX-TAIL MILLETS (*Setaria italica*, Beauv.)

ROOTS.—The seminal roots are three in number ; the adventitious roots are numerous, thin and wiry, developing from the lower nodes at ground level. All appear to function throughout the life of the plant, but their distribution in the soil is not definitely known.

STEMS.—The stems are erect and slender, from 2 to 5 feet in height ; hollow except at the nodes which are solid and somewhat swollen below. The inter-nodes are short at the base, becoming longer in the middle region, and again shorter above ; the last inter-node, which ends in the spike-like panicle, is the longest. A slight furrow, alternating in position at each node. runs for a short distance

upwards from each node. A purple pigment, variable in intensity, may be found sometimes on the nodes and inter-nodes. In its extreme form, it is present on the exposed roots, sheaths, blades, nodes and inter-nodes, and also on the peduncles, glumes and bristles. According to Ayyangar *et al.* (1935), four factors are responsible :—a basic factor P (P 1—6); a factor I, determining intensity; a factor V, determining clear manifestation of colour in the vegetative parts; and H, clear manifestation in earheads.

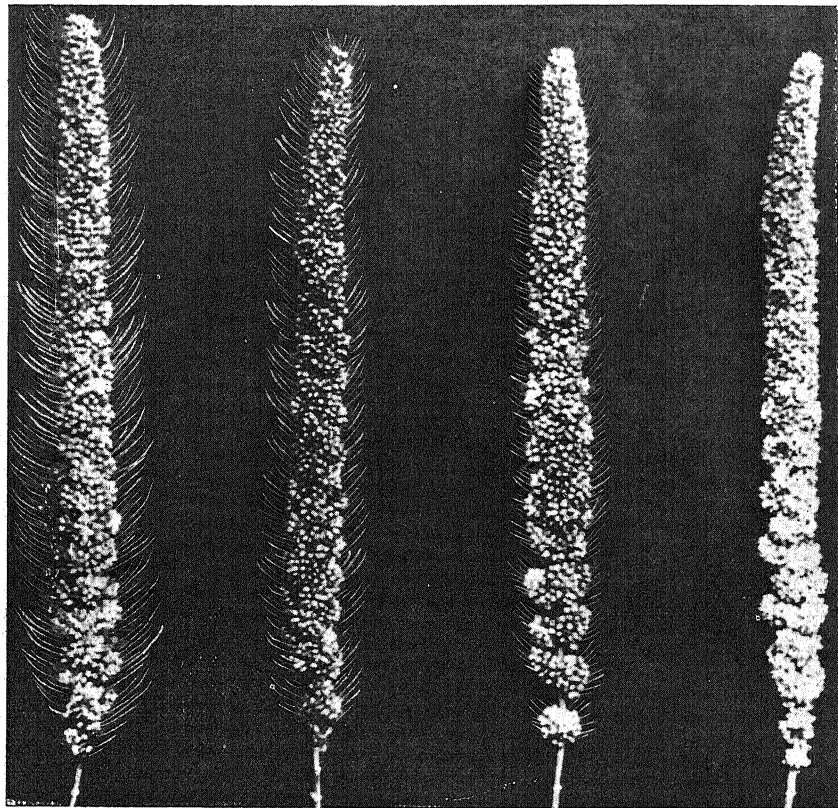


FIG. 106.

Ear-heads of *Setaria italica*, showing long, medium, short and dwarf bristles. (After Ayyangar *et al.*)

Tillers develop from the buds of the basal nodes, and in some cases true branches arise from the buds of the upper nodes.

**LEAVES.**—The leaf sheaths are in most cases, especially above, longer than the nodes. They are faintly grooved with the mid-rib fairly distinct, glabrous or slightly hairy, markedly open above and slightly overlapping towards the base. The collar is indistinct and marked by a narrow band of fine brown hair. The ligule is short, thick and fimbriated. The blades are long, broad and taper gradually to an acute point; their upper surfaces are smooth and their lower ridged, with

the mid-rib prominent. Albinism has been noted in certain strains and its inheritance studied by Rangaswami Ayyangar and Narayanan (1933).

**INFLORESCENCE.**—The inflorescences are spike-like panicles, dense or at times interrupted, varying from 2 to 9 inches long by  $\frac{1}{2}$  to 2 inches wide. The main axis is ribbed and covered with dense white cilia. The laterals are much reduced and ciliate, carrying from 6 to 12 sub-sessile spikelets, each subtended by 1 to 3 bristles, which vary in colour and length, and bear scabrid hairs throughout their length.

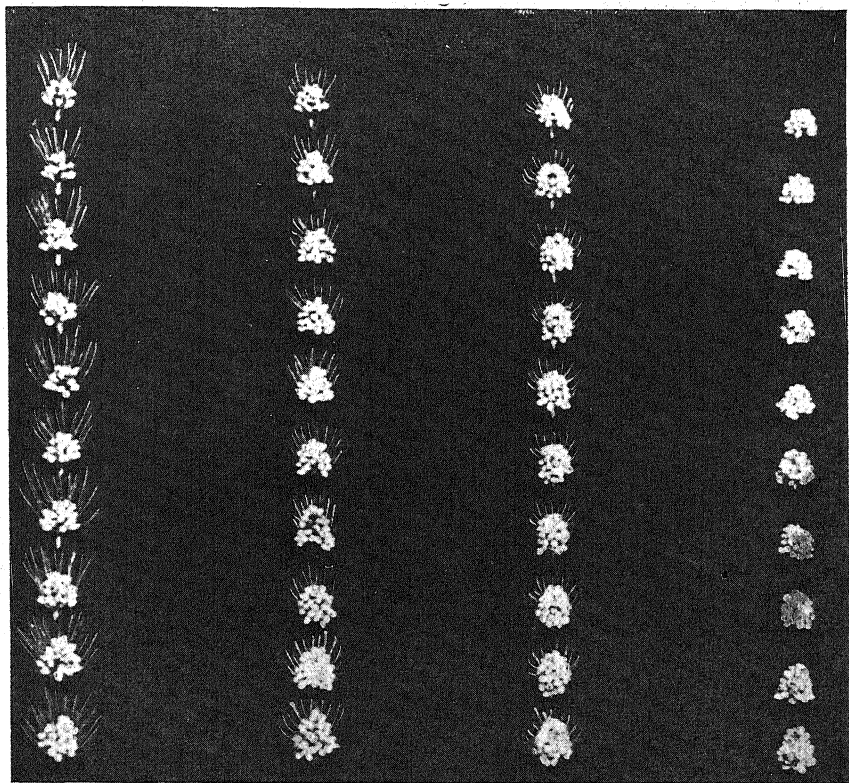


FIG. 107.

Spikelet groups of *Setaria italica*, showing long, medium, short and dwarf bristles. (After Ayyangar *et al.*)

According to Rangaswami Ayyangar *et al.* (1933), the number of bristles is usually 1 to 2, rarely 3 to 4. Higher numbers have, however, been noted. Four group lengths have been identified :—Long, from 7 to 14 mm., with an average of 10.5 mm.; medium, from 4.5 to 9 mm., with an average of 8 mm.; short, from 3 to 7 mm., with an average of 5 mm. and dwarf, from 2.2 to 4.5 mm., with an average of 3.2. The above authors have identified four factors responsible, two basic factors *X* and *E*, and two further factors,  $L^1$  and  $L^2$  inter-acting with the basic factor.

Their schema is as follows :—

Basic factors  $X_e$ , plus  $L^1$  or  $L^2$  give "short" bristles, the two forms being indistinguishable.

" " " plus  $L^1$  and  $L^2$  give "medium" bristles.

" "  $XE.$ , plus  $L_1$  give "short" bristles.

" " " plus  $L_2$  give "medium" bristles.

" " " plus  $L_1$  and  $L_2$  give "long" bristles.

It has frequently been asserted that the bristles represent abortive branches. Occasionally they bear a spikelet at the tip, indicating that they may represent aborted parts of a fascicle. Rangaswami Ayyangar *et al.* (1933) have found that the number of such spikelets may vary from 80 per cent. to nil and the expression

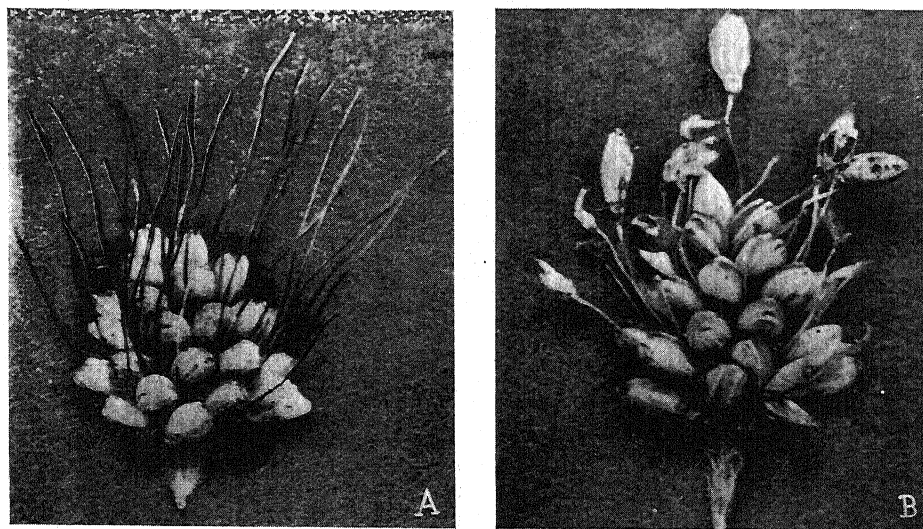


FIG. 108.

- A. Fascicle of spikelets showing long bristles.  
 B. Fascicle of spikelets with some of the bristles carrying spikelets. (After Ayyangar *et al.*)

from a small knob to one carrying a well-developed grain. They recognize two conditions :—"Stray" with low numbers and poor development, and "Full," with up to 80 per cent. of bristle-bearing spikelets and 35 per cent of those with grains. The "full" condition was found to be recessive in certain families, incompletely dominant in others.

**SPIKELETS AND FLOWERS.**—The spikelets are elliptical, usually about half the length of the subtending bristles. Each spikelet has 2 membranous glumes, a lower which is about one-third the length of the spikelet, oval-pointed and 3-nerved ; and an upper which is nearly as long as the spikelet, broadly oval, pointed and 5-nerved. Frequently the glumes are tinged with purple. Within the glumes are 2 flowers, the lower sterile, the upper perfect. The lower sterile flower is represented by a 5- (in certain types 7-) nerved, membranous, elliptical and obtuse

lemma ; and at times a much reduced membranous palea. The lemma of the fertile flower is 5-nerved, broadly oval, chartaceous in texture, and when ripe is very variable in colour with a dull or shining surface. The palea is about as large as the lemma and of similar texture. There are 2 broad cuneate lodicules ; 3 stamens, with orange or white anthers ; a smooth oval ovary, with 2 long styles, each terminating in a brush-like stigma.

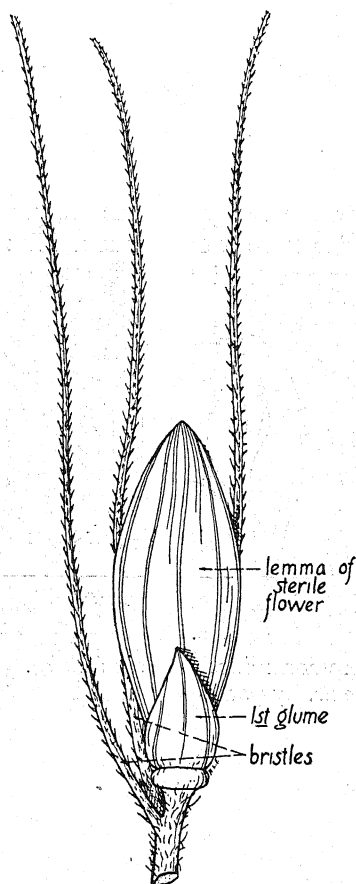


FIG. 109.

Spikelet of fox-tail millet (*Setaria italica*). X 15. (After Robbins, *Botany of Crop Plants*, by permission of P. Blakiston's Son & Co.)

A majority of the flowers open, and self-pollination is the rule, though cross-pollination may occur.

The mode and time of flower opening have been studied by Hosino and Tutumi (1926), and also by Rangaswami Ayyangar *et al.* (1933). The period of flower opening, according to the latter, extends over a period of 10 to 15 days and is unaffected by the season. The maxima of flower opening are to be found between 10 p.m. and midnight and between 6 a.m. and 8 p.m. During the hot season in India the first two flushes are approximately equal in extent, but in the cold season,



the morning flush is only half as intense as the night. Humidity and temperature appear to be the chief controlling factors.

**MATURE GRAIN.**—Lemma and palea firmly enclose the mature grain. The colour varies—yellow, pale straw colour, orange, red, pink, brown and black seeds are all met with. In some, the seed is shining and polished with only indistinct transverse ridges; in others, the seed has a dull appearance due to the presence of minute elevations on the hull. The genetics of the grain colour has been studied by Rangaswami Ayyangar and his co-workers (1931).

The caryopsis proper is broadly oval, smooth and white. The ventral surface is flattened with a dark-coloured spot, the hilum, at the base; the dorsal is convex, with a groove which extends half-way from the base marking the position of the embryo. The pericarp is thin, its cross and tube cells very similar. The testa is a single layer with large cells and beaded walls. There is a single aleurone layer and an endosperm whose elongated cells are packed with polygonal starch grains. These starch grains have a conspicuous hilum; they are small to the exterior, conspicuously larger to the interior.

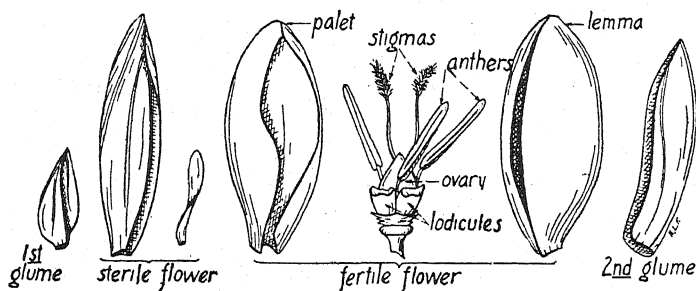


FIG. 110.

Dissected spikelet of common millet (*Setaria italica*). X 10. (After Robbins, *Botany of Crop Plants*, by permission of P. Blakiston's Son & Co.)

**CHROMOSOME NUMBERS.**—The diploid chromosome number is stated to be 18 (Morinaga *et al.*, 1929), since verified by Krishnaswami *et al.* (1935). These authors found *S. verticillata*, Beauv., to have the same number, and both to possess one chromosome pair larger than the others.

**CLASSIFICATION.**—There are two groups of Fox-tail Millet, the small and the large-headed types, but the varieties within these are difficult to distinguish. The following key, based on Frear's, gives the more important diagnostic characters.

KEY TO PRINCIPAL TYPES OF FOX-TAIL MILLETS (*Setaria italica*).

- A. Heads small, uniform, compact, seeds yellowish to black with usually a large percentage very dark; beards brown or purple . . . . . *Hungarian Millet.*
- AA. Heads large, more or less open; seeds more or less bunched.
- B. Heads long, slender, very open, lax, drooping: seed groups very distinct . . . . . *Aino Millet.*

BB. Heads shorter and plumper, bushy, erect or slightly drooping: seed groups indistinct.

C. Seeds yellow.

D. Profusely bearded; medium large heads

E. Heads large, seeds small, seed groups more distinct

*German Millet.*

EE. Heads small, seeds large, seed groups less distinct

*Common Millet.*

DD. Sparingly bearded; heads very large

*Golden Wonder Millet.*

CC. Seeds red or pink

*Siberian Millet.*

A key to the sub-species has also been given by Hubbard (1915), and Woodhouse and Ghosh (1921) have described certain of the varieties grown in Bengal. The types cultivated in Georgia have been discussed by Dekaprelavitch and Kasparian (1928).

#### PEARL MILLET (*Pennisetum typhoides*, Stapf and Hubbard.)

**ROOTS.**—Pearl millet produces only one seminal root. The first of the secondaries consists of a pair of roots which develop at the first node in a plane at right angles to the plane of the first axillary bud. At the next node, a second pair similarly develops: thereafter, a whorl of 4 to 6 roots is produced at each node. A brief description of the extent of the root system and of the root anatomy is given by Godbole (1927).

**STEMS.**—The stems are erect, cylindrical and solid, 3 to 8 feet in height. The upper inter-nodes are long, glabrous and furrowed on the side next the leaf blade. The nodes are marked by a ring of long white cilia pointing upwards.

Buds develop at the nodes in the axils of the leaves. Those at ground level may develop as suckers; above ground, they may develop from above downwards as true lateral branches, each of which may produce a terminal "head".

**LEAVES.**—The leaf sheaths may be slightly longer or shorter than the inter-nodes. They are markedly open above, overlapping at the base, faintly grooved and glabrous. The collar is distinct, purple in colour, with a fringe of whitish projecting cilia at the base of the pigmented area. The ligule is short and fimbriated. The leaf blades are broad and lanceolate; long and pointed; the mid-rib well developed and so preventing the blades from drooping; both surfaces are faintly ridged, the upper scabrid and at times long-hairy, the lower smoother and usually glabrous. According to Godbole (1927) stomata are found on both leaf surfaces, in approximately equal numbers. The counts for the lower surface varied from 50 to 80 per square millimetre.

The prophyllum of the lateral branches resembles that of *Sorghum*.

**INFLORESCENCE.**—The inflorescence is a terminal dense cylindrical and spike-like panicle, 5 to 14 inches long by  $\frac{3}{4}$  to  $1\frac{1}{4}$  inches wide. The rachis is erect, cylindrical and beset with fine white hairs. The spikelets are in groups of 1 to 4,

usually 2, subtended by and deciduous with a cluster of long scabrid and plumose bristles, the whole carried on a short lateral axis which, like the rachis, is covered with white silky hair. The number of bristles varies from 40 to 50. In most types, they are almost as long as the spikelets, slightly curved and scabrid; in a few forms, however, the awns may be markedly longer than the spikelets.

**SPIKELET.**—The lower glume is short and broad, membranous, and truncate, with the upper margin somewhat fimbriate. The upper glume is about

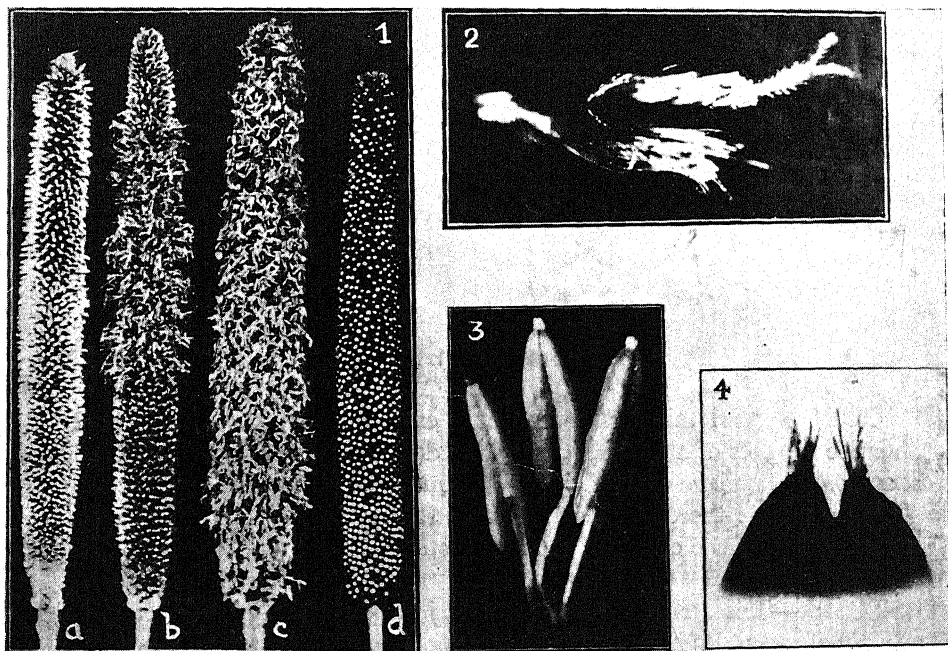


FIG. III. Anthers in *Pennisetum typhoideum*.

1. a. Protogynous conditions. b. First wave of anther production from bisexual flowers. c. Felt of persistent dry anthers. d. Set grain.
2. Hermaphroditic flower with stigma and anthers just emerging.
3. Penicillate anthers.
4. Pencils enlarged. (After Ayyangar *et al.*)

half the length of the spikelet, slightly longer than broad, truncate and somewhat 2-cleft with the margins fimbriate. There are 2 flowers, the lower normally staminate (at times infertile, absent, or rarely perfect); the upper perfect. The lemma of the lower flower is oblong, acuminate, 5- to 7-nerved, and sparsely hairy; the palea is small, membranous or absent; the lodicules are absent and there are 3 stamens. The lemma of the perfect flower is oblong lanceolate and 2-nerved; the palea is hyaline and narrowly oval; the lodicules are absent; the stamens are 3 in number; the ovary is obovate, smooth, with two styles which are generally connate at the base. The structure of the ovule and embryo-sac, etc., has recently been studied by Rangasami (1935).

**ANTHESIS AND POLLINATION.**—The flowers above the middle of the panicle are the first to open, anthesis thereafter spreading upwards and downwards. The perfect flowers open first, followed by the staminate. Cross-pollination is said to be normal. According to Godbole (1927) this is due to marked protogyny. The styles develop first, each style requiring 36 to 48 hours to attain their maximum length (5 to 7 mm.) and remaining capable of being pollinated for a day or two thereafter. After the styles begin to dry up the anthers begin to appear. There is, however, a certain overlapping at the base of any one inflorescence.

Rau (1929) reported 14 as the diploid chromosome number: Rangasami (1935) found 7 bivalents at meiosis, with 3 chiasmata at diplotene, but only 2 terminal chiasmata per bivalent at diakinesis.

**MATURE GRAIN.**—At maturity, the caryopsis just protrudes beyond the lemmas, and readily becomes free. The colour varies from white to pale blue. It is 3 to 4 mm. long, obovate, pointed at the base, rounded at the apex with a trace of the style laterally exerted. The embryo, which is fairly obvious, lies on the ventral face and on the base of the dorsal face is an oval brownish scar.

#### FINGER MILLET (*Eleusine coracana*, Gaertn.)

Finger Millet is cultivated in India and in Africa by the natives, both for grain and forage. It is closely related to and perhaps derived from the ruderal grass, *Eleusine indica*, which is found throughout the sub-tropical regions of the Old World, and has been introduced into similar regions of the New.

The stems are erect or slightly kneed, compressed and glabrous. The leaves are numerous and distichous; the sheaths compressed, open, striate, glabrous and with more or less ciliate margins; the ligules are short, membranous and fimbriate; the blades are linear and tapering to an acute point, folded and striate, glabrous except at the often ciliate margins.

**INFLORESCENCE.**—The inflorescence is a terminal umbel of 2 to 10 straight, thick sessile spikes 1 to 5 inches long, usually with 1 to 2 (rarely more) additional spikes,  $\frac{1}{4}$  to 3 inches below. Each rachis is angular, pubescent to villous at the base, but glabrous above.

**SPIKELETS.**—The spikelets are often curved, crowded, 2- to 10-flowered. The lower glume is ovate, obtuse and keeled with 2 lateral nerves close to the keel. The upper glume is very similar but slightly longer. All flowers are perfect, except the terminal which may be only staminate or infertile. The lemmas are broadly ovate, acute and 3-nerved. The paleas are somewhat shorter than the lemmas, 2-keeled with the keels winged. There are 2 lodicules, broad and truncate; 3 stamens; an obovate ovary with distinct styles and plumose stigmas. The grain is oblong, reddish-brown with finely curved striæ, and falls free at maturity. Cases of polyembryony have been recorded and described by Rangaswami and Krishnaswami (1930). Rau (1929) gave the chromosome number as ca. 36, since verified by Krishnaswami (1935). The basic number of the genus appears to be 9, and *E. coracana* is therefore tetraploid. Rangaswami Ayyangar and his co-workers have published a series of papers on the genetics of this plant (1929; 1931; 1932; 1933).

**BROOM-CORN OR PROSO-MILLET (*Panicum miliaceum*, L.)**

Proso-millet is an annual, which is extensively grown in the Eastern Tropics.

**ROOTS.**—The seminal roots are few in number, and are followed later by whorls of adventitious roots from the nodes near ground level.

**STEMS.**—The stems are erect, at times decumbent at the base, 5 to 6 noded, 1 to  $3\frac{1}{2}$  feet high. The inter-nodes are short and hollow, cylindrical or slightly compressed, with a slight alternating furrow at the base ; they are glabrous towards the base, rough-hairy above and especially just below the node.

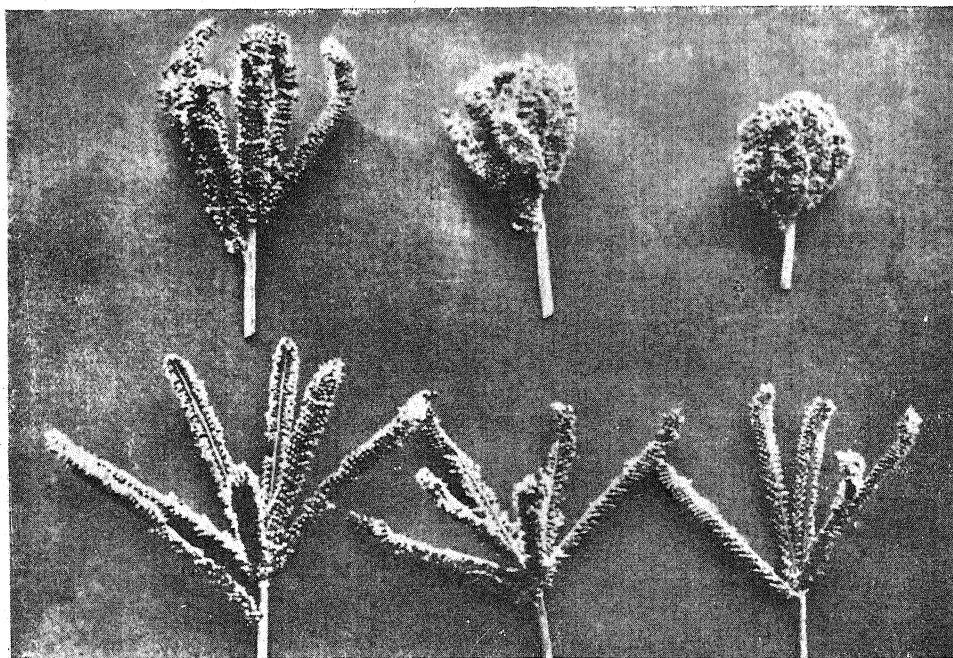


FIG. 112. Types of ear found on Finger Millet, *Eleusine coracana*.

Above : Top-curved ; Incurved ; Fist-like.

Below : Long open ; Short open ; Very short open. (After Ayyangar *et al.*)

The plants tiller to a minor extent, and true laterals, often bearing panicles may develop from the buds at the upper nodes.

**LEAVES.**—The leaf sheaths are open and slightly ridged, with short dense hairs at the nodes, more scattered stiff hairs above, the latter mounted on a small papilla. The collar is indistinct and the auricles absent. The ligule is short, thick and fimbriated. The leaf blades are 5 to 10 inches long by  $\frac{1}{3}$  to 1 inch wide, in outline linear-lanceolate, with scattered hairs especially on the upper surface. An anthocyanin pigment may be present on the leaf sheaths and leaf margins. When present, it is also found on the glumes and stigmas. These types show simple dominance to pure green types (Kadam, 1935).

**INFLORESCENCE.**—The inflorescence is a rather dense panicle, 4 to 10 inches long, equilateral or unilateral, and at times much compressed. The main axis is slender, striate and glabrous; the laterals alternate, erect or ascending, 3- to 5-nate, filiform, angular and hairy. The pedicels are unequal, scabrid and swollen at the apex.

**SPIKELET.**—The spikelets are oval and acuminate, 4 to 5 mm. long. The lower glume is broad, clasping, acuminate, 5- to 7-nerved, from half to two-thirds the length of the spikelet; the upper glume is as long as the spikelet, oblong, sub-acuminate, concave at the base, up to 13-nerved. There are 2 flowers, the lower sterile, the upper perfect. The sterile flower is represented by its lemma and palea, the former resembling the second glume, but 7- to 13-nerved; the latter much reduced. The fertile upper flower has a broad obtuse lemma, 7-nerved, becoming coriaceous, smooth and shining; its palea is broad, 3-nerved, becoming coriaceous, shining, and light brown in colour.

There are 2 lodicules, short, broad and truncate. The stamens are 3 in number and the ovate ovary has two styles ending in plumose stigmas. Broom-corn millet according to Youngman and Roy (1923) is mainly self-pollinated.

Rau (1929) gave the diploid chromosome number as 42; Church (1929) reported 40.

**MATURE GRAIN.**—The caryopsis is enclosed in the hardened, shining lemma and palea, the whole measuring about 3 mm. long by 2 mm. broad. The naked grain is broad by oval, smooth and white, and possesses no furrow.

The characters of many of the varieties have been studied by Arnold (1914, 1927) and Lewicki (1921, 1929).

### JAPANESE BARNYARD MILLET (*Echinochloa frumentacea* (Roxb.) Link.)

This type is probably derived from and is undoubtedly closely allied to the widely distributed ruderal species, *Echinochloa* (*Panicum*) *crus-galli*, Beauv.

**ROOTS.**—The seminal roots are 3 in number; the adventitious roots are numerous, somewhat stout, and finely branched throughout their length.

**STEMS.**—The stems are glabrous and smooth, 1 to 3 feet high; at times slightly geniculate, compressed below, rounded above, except near the node, where they are slightly and for a short distance, flattened but not furrowed. The lower buds may develop as tillers; the upper as true lateral branches.

**LEAVES.**—The sheaths are generally as long as the inter-nodes, often compressed below, open, striate and glabrous. There is a V-shaped collar with no auricles and no ligule. The blades are linear with a wide base, tapering to an acute point; both surfaces are slightly ridged, the upper scaberulous, the lower slightly so; the margins are cartilaginous with fine teeth.

**INFLORESCENCE.**—The inflorescence is paniculate, the main axis 3- to 5-angled, striate and scabrid, with 5 to 15, usually solitary, distant, except the uppermost, suberect or spreading lateral branches, forming rather dense simple or subsimple, subsecund false spikes. The rachises of the laterals are triquetrous and scabrid, with coarse bristles especially at the nodes.

**SPIKELETS.**—The spikelets are usually crowded on short, fascicled or 2-nate, scabrid pedicels, bristly at the base and discoid above. There are 2 glumes, the lower membranous, tinged with purple, broadly ovate and clasping at the base, obtuse to sub-cuspidate, 3- to 5-nerved, finely scaberulous, about one-third the length of the spikelet; the upper green below, purple above, broadly ovate-oblong, concave, acute or sub-cuspidate, as long as the spikelet, pubescent except on the line of the 5 nerves which are scabrid below, becoming spinulous above.

The lower floret is infertile, the upper perfect. The lemma of the lower flower resembles the upper glume, but is generally depressed on the back, 7-nerved, and cuspidate; its palea is elliptical and much shorter than the lemma. The perfect flower has a sub-coriaceous ovate 5-nerved lemma; a 5-nerved palea; 2 lodicules; 3 stamens with purple anthers; and an ovate ovary with distinct styles ending in plumose stigmas. The chromosome number was first reported as ca. 48 (2n). According to Church (1929) the haploid number is 21: Avdulov (1931) found 54 (2n): Hunter (1934), 36. As the basic number of the Paniceae is 9, Avdulov's and Hunter's figures would appear to indicate polyploidy.

**MATURE GRAIN.**—The mature grain is firmly enclosed in the white, shining and hardened lemma and palea.

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## CHAPTER IX

### SACCHARUM Sp.—THE SUGAR CANES

THE genus *Saccharum* includes several species of perennial tropical grasses, chiefly Asiatic.

The plant as now grown exists in several distinct types or varieties, so distinct indeed that they may with justification be treated as three or four sub-species, if not species. Certain of the forms are now also known to be hybrids. The following description is in the main generalized.

**HABIT.**—Sugar cane is a perennial grass which stools prolifically from the base. It is grown for its juice which should, according to Leather, yield up to 70 per cent. in the mill and contain at least 15 per cent. of cane sugar and not more than 17 per cent. of glucose.

**ROOTS.**—On germination a single seminal root is produced, which grows until it is a few millimetres long and is then replaced by a secondary root. Similar roots follow and later a series of adventitious, fibrous roots develop in whorls at the lower nodes, situated below, at ground level and immediately above ground level. In time the adventitious roots produce lateral branches which are much thinner than the primaries. The tips of all are protected by root caps, often red in colour.

Lee (1926) conducted a quantitative study of the distribution of the root system in Hawaii. His method consisted in selecting five representative stools of the variety to be studied, which were then cut level with the soil. The area occupied by the plants was then enclosed and the soil carefully excavated to a depth of 8 inches. This soil was then passed through a  $\frac{1}{4}$ -inch-mesh sieve and all the roots removed, washed, dried and weighed. The process was then repeated for each successive 8-inch stratum down to a depth of 40 inches.

With plant canes, H109, 10½ months old, and growing in furrows, the following results were obtained :

TABLE XXIX.  
ROOT WEIGHTS OF SUGAR CANE.  
(Data from Lee.)

	<i>Weight of roots in gr.</i>	<i>Per cent. of Total Weight.</i>
First 8 inches .. ..	135·2	70·1
Second 8 inches ..	43·9	22·8
Third 8 inches ..	11·3	5·9
Fourth 8 inches ..	2·3	1·2

Comparative studies under varying conditions were also conducted. The results indicated that the majority of the roots occur in the upper soil levels. Canes grown in furrows showed more than 58 per cent. of the roots in the first 8 inches. Canes grown on ridges (hilled-canes) showed under 20 per cent. in the first 8 inches, over 40 per cent. in the second 8 inches. A normal crop under irrigation was calculated to leave 0.9 to 1.85 tons of dry organic matter in the soil.

Venkatraman and Thomas (1922, 1928) have studied the development of the root systems in several forms, mostly Indian, at different stages of growth. When

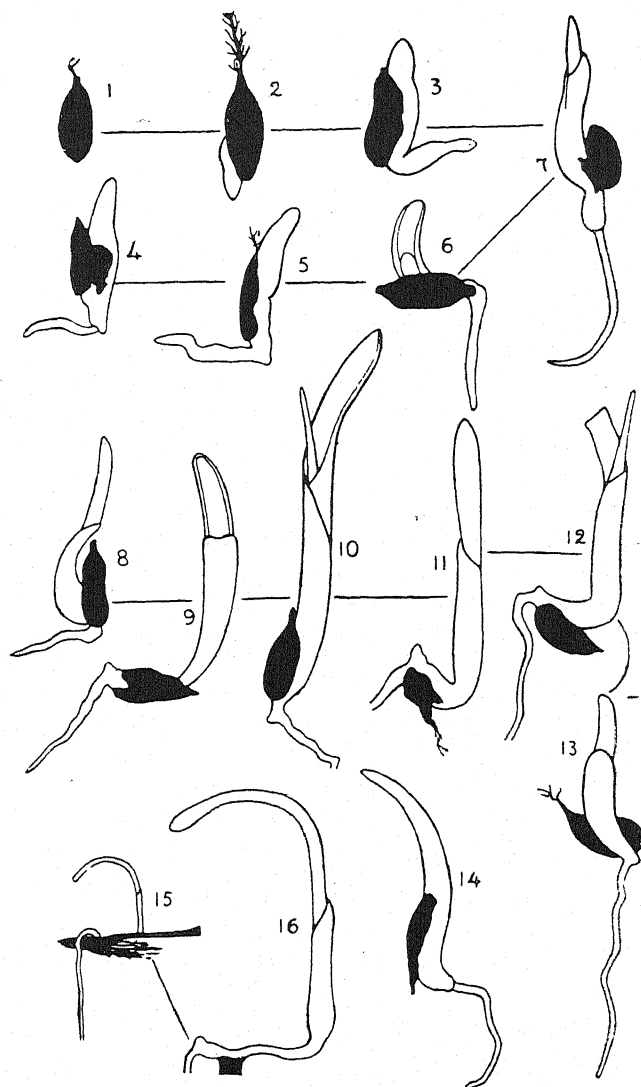


FIG. 113. Early stages of Germination of the seed.

1 to 7. Seedlings of Kassoer, 4 days old. 8 to 13. Eight days old. 14. Louisiana, 6 days old. 15 to 16. Madras seedling No. 2, 13 days old. (After Barber.)

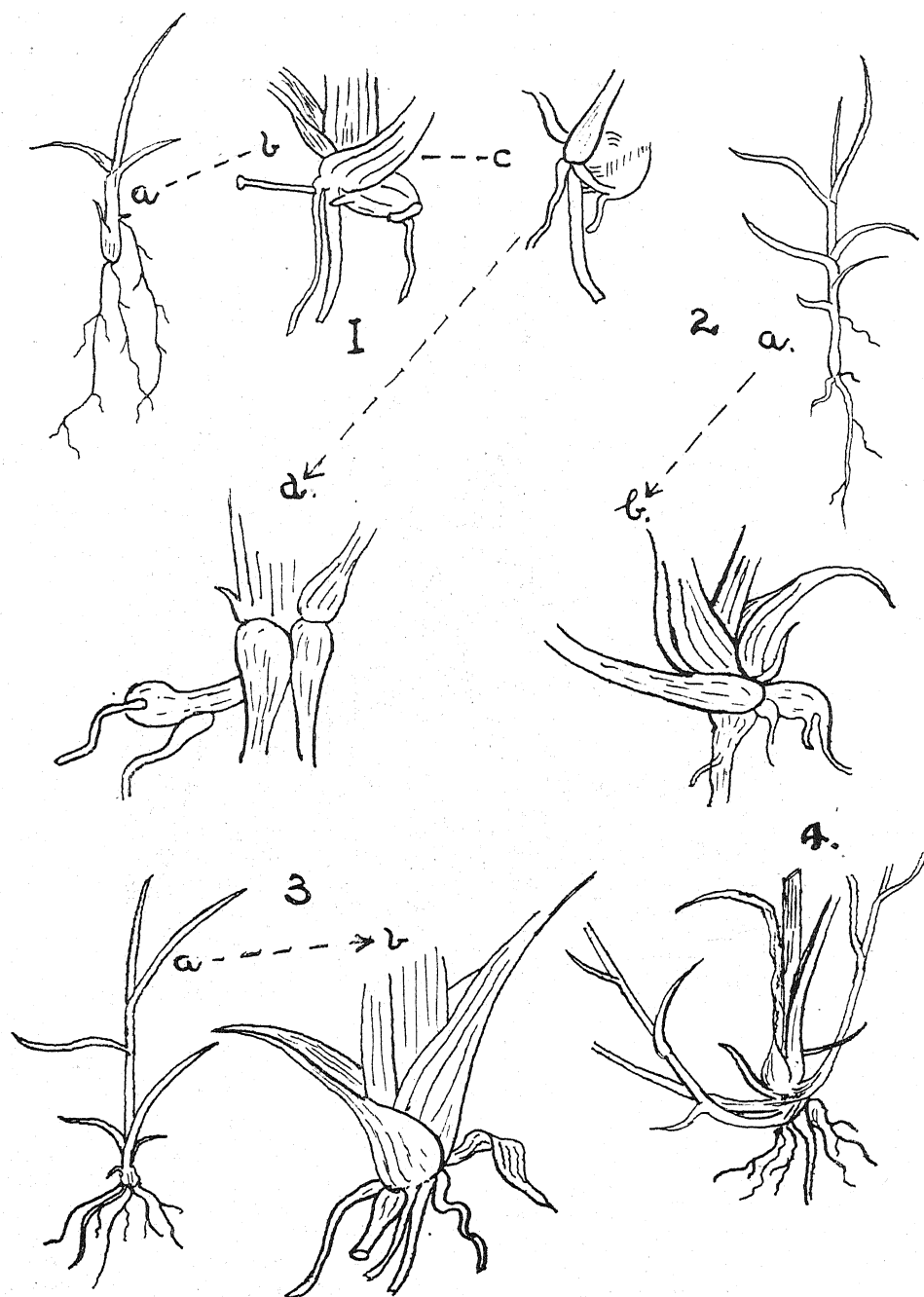


FIG. 114. Stages in the development of the seedling ("Karun").  
1 to 4 from 1 inch to 1 foot in height. (Redrawn with modifications after Barber.)

the “sets” are planted, adventitious roots develop from the root-ring or “keimring”. The number of these “set roots” varied with the variety. Tropical canes on the whole produced fairly large numbers (13.9 to 56.2); the Indian canes in general had lower numbers (1.5 to 15.5). *S. spontaneum* also developed but few (avg. 2.3). These “set roots” function for a time and then die, being replaced by the “shoot roots” which develop from the shoot and its tillers.

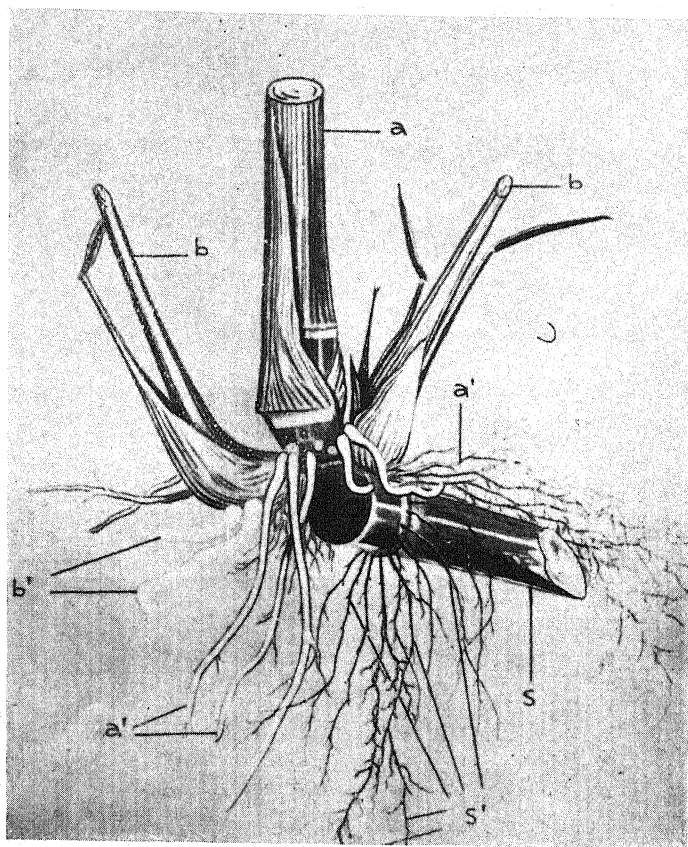


FIG. 115. “Set” and “shoot” roots.

- S. The original planted set. S'. Set roots formed from the set. a. The first shoot from the set. a'. Shoot roots developed from a. b. Lateral shoots from a. b'. Shoot roots from the laterals b. (After Venkatraman and Thomas.)

The period of time during which the “set roots” function, however, varies with the variety. Varietal differences in the rate of development of the “set roots” are also met with. The Sareta and Pensali groups develop more rapidly than those of the Sunnabile and Mungo groups. The latter develop very slowly, in some of the types starting only after the shoots have appeared above ground.

Like the “set roots” the “shoot roots” also tend to die, being replaced by newer roots from higher nodes of the same shoot and from the nodes of later formed tillers. Finally, the adult root systems appear to vary markedly. Most tropical

canes have shallow systems. The Indian canes studied tend to vary. Varieties of the Sareta and Mungo groups have relatively deep systems; those of the Pensali group are shallower. *S. spontaneum* exceeded the others considerably, apparently reaching depths of over 6 feet.

**ROOT ANATOMY.**—The root structure has been studied in part by Barber (1915-19), Klinge (1879), Bremekamp (1914), and more generally by Artschwager, (1925).

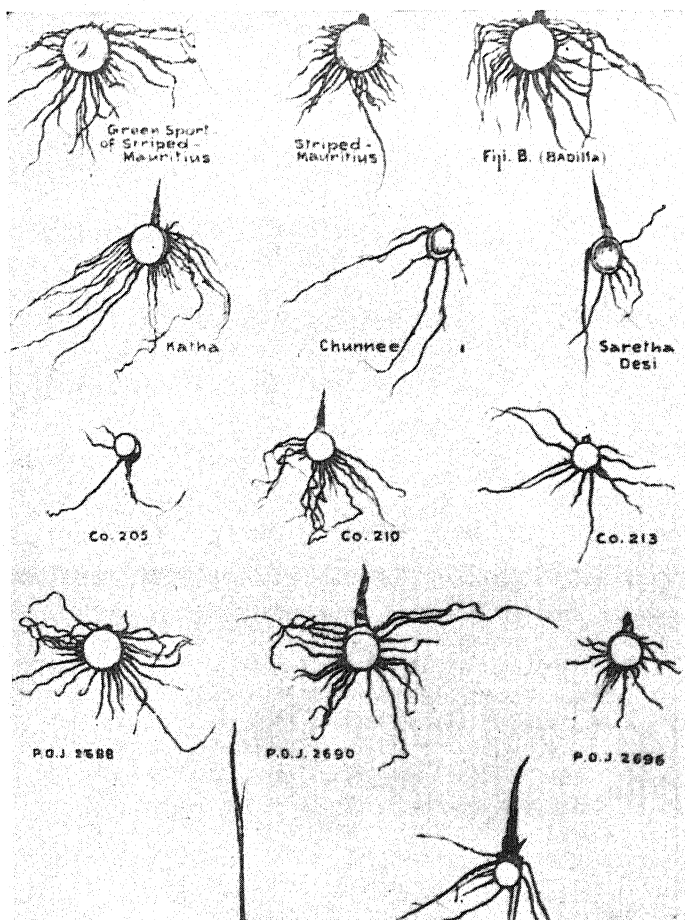


FIG. 116.

Relative development of set roots in 12 cane types (16 days after planting). (After Venkatraman and Thomas.)

A cross-section of a young root is bounded externally by a continuous epidermis. Many of the cells grow outwards as root hairs which may remain attached to the root long after they have ceased to function. Beneath the epidermis a single layer of cells, larger and more elongated than those of the epidermis, constitutes the exodermis. Their walls are suberized and their inner tangential surfaces thickened. A distinct sclerenchymatous cylinder of several rows of

cells follows. The remainder of the cortex consists of large loosely-packed parenchymatous cells with small inter-cellular spaces. The endodermis bounds the vascular cylinder and forms a single uninterrupted layer. Each cell is a vertically elongated 4-sided prism with horizontal ends. Their radial walls may be longer than their tangential. All the walls are at first thin, but later the inner tangential walls and parts of the radial walls become markedly thickened and lignified. Their inner tangential walls are also pitted and may develop peculiar protuberances whose tips contain silica (Klinge, l.c., Bremekamp, l.c.).

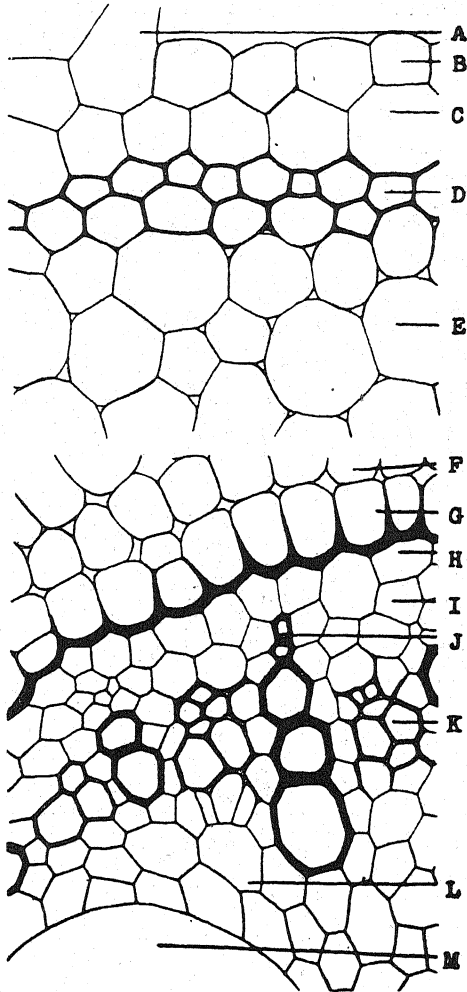


FIG. 117. Cross-section of part of young root.

A, Root hair; B, epidermis; C, exodermis; D, sclerenchyma tissue; E, part of cortex; F, inner cortex; G, endodermis; H, pericycle; I, interstitial parenchyma; J, protoxylem; K, phloem group; L, parenchyma between protoxylem and large pitted vessel; M, large pitted vessel (still in meristematic condition). (After Artschwager.)

The central cylinder is bounded by a delicate pericycle, but in the seminal root and young lateral roots the xylem may abut on the endodermis. The vascular tissue consists of alternating groups of primary xylem and phloem. These xylem plates are few in number and may reach the centre in seminal and young lateral roots; in all others they are numerous and do not reach the centre which is filled by a massive pith. At the margin of this pith a ring of eight large vessels, becoming more numerous in older roots, is found.

Proto-xylem and phloem are separated from one another by interstitial parenchyma; similar cells separate these tissues from the large vessels and in turn surround the latter to form a peripheral sheath adjoining the pith. The cells of this sheath become thickened and lignified at an early date.

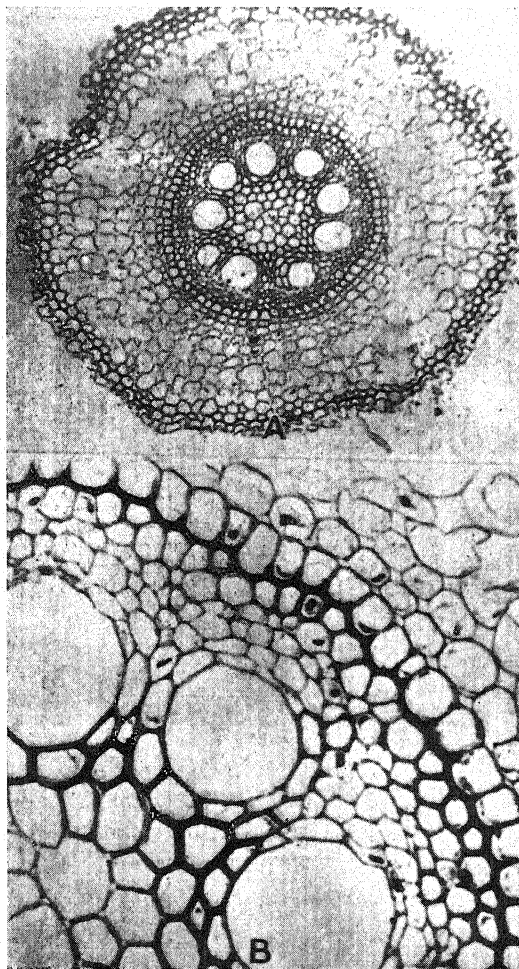


FIG. 118.

- A. Cross-section of older root. X 100.  
B. Part of A enlarged, showing details of endodermis and vascular tissue. X 450.  
(After Artschwager.)

The first element of the proto-xylem is a narrow vessel with scalariform or spiral-reticulate thickenings. Later elements are larger, but similar.

The phloem groups are small and consist of square or pentagonal cells with somewhat thick, highly refractive walls.

In older roots marked thickening and lignification of all the tissues of the central cylinder (with the exception of the phloem) takes place. The cortical cells bounding the endodermis also lignify and in course of time the parenchymatous cortical tissue disintegrates leaving strands of cortex which stretch radially from the exodermis on the outside to the lignified inner cortex on the inside.

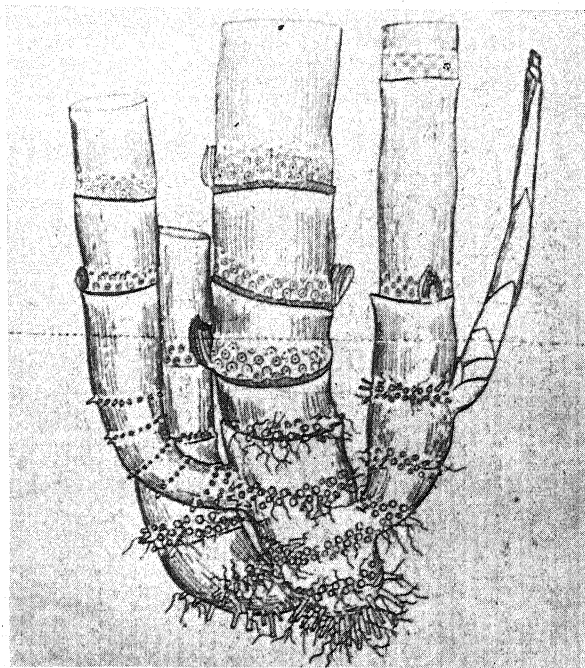


FIG. 119.

Part of stool of large sugar cane. (After Artschwager.)

**STEMS.**—The stems of the sugar cane vary from 8 to 15 feet or more. They are clearly divisible into a series of nodes and inter-nodes. The number of the nodes is subject to considerable variation in the different varieties. They are commonly thinner than the inter-nodes and immediately above each there is a distinct root-ring or "keimring" bearing several rows of root primordia and a single bud, succeeded by a narrow intercalary meristematic zone responsible for the elongation of the inter-node.

The inter-nodes increase in length from below upwards, but towards the apex they again shorten. The last inter-node passes insensibly into the main axis of the large open panicle. The nodes are more or less equal in diameter, tapering gradually towards the apex, but below ground narrowing rapidly, forming a short straight or somewhat curved cone. In outline they are either cylindrical or



barrel-shaped ; varieties slightly concave towards the middle of each inter-node or slightly tapering from the base to the apex, are also found. The colour may exhibit marked variation, and the more exposed surfaces, though hairless, are covered with a wax deposit in the form of densely crowded rods.

**TILLERING.**—At each node of the axis, a bud occurs in the leaf axil. It is generally situated at the leaf scar, but may be inserted slightly above it. Buds may

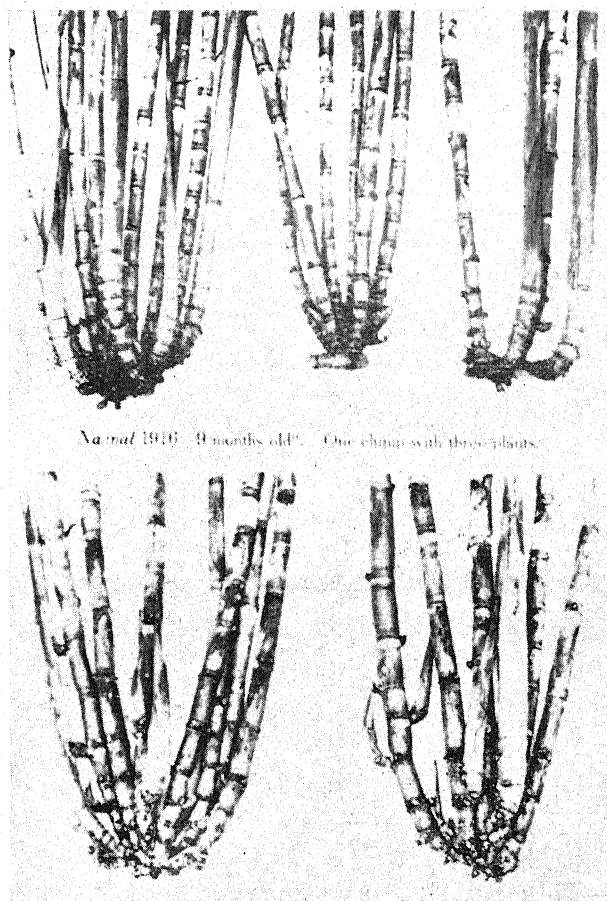


FIG. 120. Stools of Sunnabile group of Canes.

Above : Naanal, 1916 (9 months old). One clump with 3 plants.

Below : Sunnabile, 1916 (9 months old). One clump with 2 plants. (After Barber.)

be small, intermediate or fairly large, and either rounded, truncate or pointed. Distinct flanges may sometimes be present on the prophyllum. Hairs in the form of bristles, etc., may also be present.

The basal buds, as in other grasses, may develop in succession into the branches or tillers. The number of these varies markedly in different types and Barber (1919) has made an intensive study of their origin and number in the

Indian canes. By dissecting a large number of varieties and counting the number of branches produced, he obtained a series of formulae for the various groups.

**ANATOMY OF THE STEM.**—The anatomy of the stem has been discussed by several investigators, but the most complete account is that of Artschwager (1925), using one of the Noble canes (Louisiana Purple = Black Cheribon) of the species *S. officinarum*.

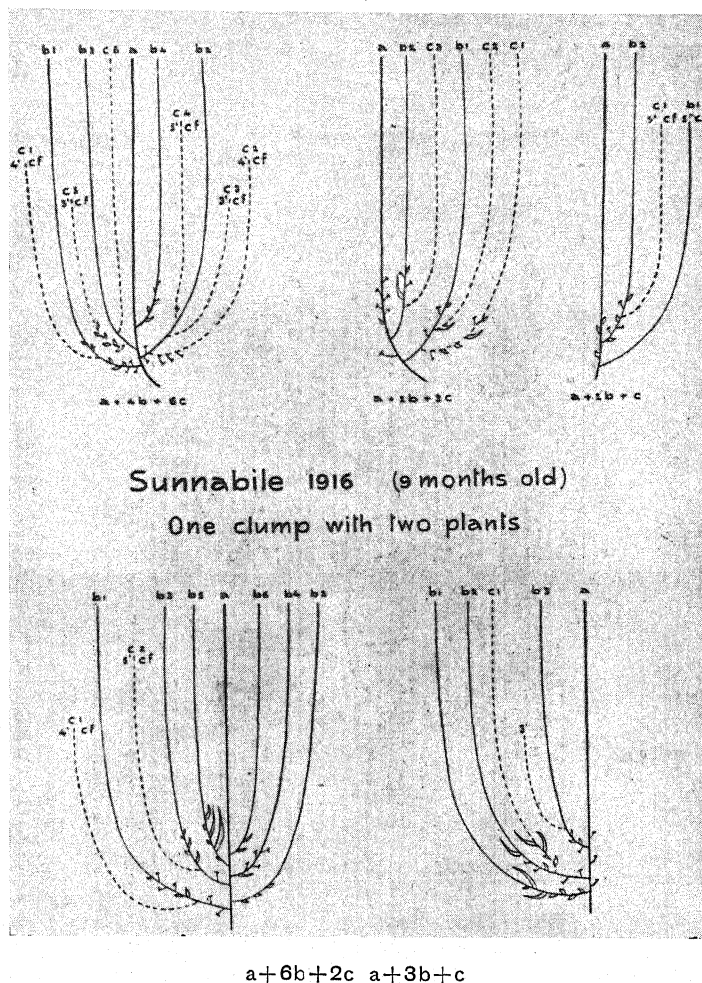


FIG. 121. Diagrammatic representation of the Tillering of the plants in Fig. 120. Above: Of Naanal (9 months old). One clump with three plants. Below: Of Sunnabile, 1916 (9 months old). One clump with two plants. (After Barber.)

a. AT THE INTER-NODES.—Externally the stem is limited by a continuous single layer of epidermal cells, interrupted by the presence of a limited number of stomata. Two types of cells are present—elongated rectangular cells and short cells occurring singly or in pairs. Typically these cells alternate, but one

or both of the short cells may be absent, producing a continuous row of elongated cells. Artschwager (1930) has studied in detail the variation of the epidermal cells in several forms. (See also, Wieler, 1898 ; Mameli de Calvino, 1922.)

The long cells form 4-sided prisms, with undulating walls which are markedly thickened, cuticularized and traversed by numerous pits. Their middle lamellae are strongly silicified.

Short cells typically occur in pairs; two short-cell groups, however, may frequently coincide by the omission of a long cell ; rarely the short cells are single. Of the members of a pair, one is larger, stains a deep golden yellow with chloroiodide

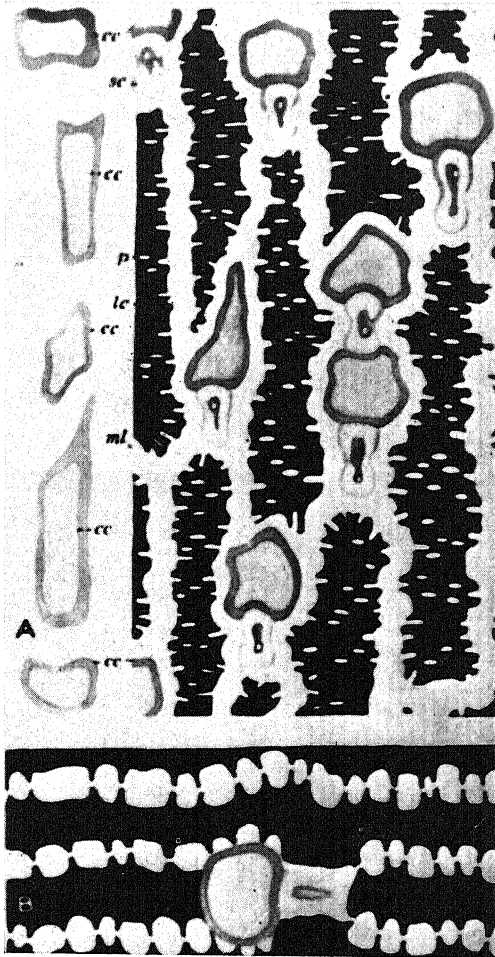


FIG. 122.

- A. Surface view of epidermis of Louisiana Purple stained with chloroiodide of zinc. X 1,000. *cc*, Cork cell ; *ml*, middle lamella of long cell ; *p*, pit ; *lc*, long cell ; *sc*, silica cell.
- B. Surface section of epidermis of Cayana. X 1,000. Notice the large number of pits in the walls of the long cells. (After Artschwager.—Original in colour.)

of zinc and is known as a "cork cell"; the other is smaller, more uniform, glistening white in appearance, and known as a "silica cell".

"Cork cells" are usually broadly reniform with the longer diameter parallel to the axis of the stem. Often they are square or rectangular; at times trapezoidal, triangular or much elongated. Such elongated cells may approximate in appearance to silica cells. Normally, the walls of the cork cell are thin, suberized and silicified; their lumens are large and contain a solid deposit of some organic substance.

"Silica cells" are normally very uniform in outline and generally rectangular with the long diameter parallel to the axis of the stem. They may, however, be broader than long, oval or round. They are practically solid, though the centres may show small air-spaces often arranged in a row. At times the silica cell may be wanting. (Fig. 122.)

The following table from Artschwager (1930) indicates some of the epidermal characters to be found in certain varieties.

TABLE XXX.  
NUMBER AND SIZE OF EPIDERMAL CELL TYPES.  
(Data from Artschwager.)

Variety.	Average width of cells $\mu$ .	Number of short cell groups per square millimetre.	Pointed elongated cells.	Solitary cork cells.	Number of stomata per microscopic field. a.
Louisiana Purple....	10.0	$\pm$ 928	Absent..	Scarce ..	1-2
D-74 .....	7.7	$\pm$ 1,112	.. do. ..	.. Abundant	14
Yellow Caledonia....	9.1	896 — 780..	Present..	.. do. ...	.. 1 or less
P.O.J.:					
2714 .....	10.6	816 — 916..	Absent..	.. do. ...	.. 10.
36 .....	13.54	$\pm$ 528..	Present..	Absent....	.. 12.
213 .....	11.25	$\pm$ 372..	do. ..	.. do....	.. 1.
234 .....	12.5	376 — 484..	.. do. ..	.. do. ...	.. 4.
Kassoer .....	13.3	364 — 480..	Scarce ..	Scarce ....	.. 1.2.
U.S.:					
663 .....	12.5	480 — 540	Absent	Abundant	1.
833 .....	13.3	$\pm$ 656	do.	Absent	15.
759 .....	13.6	428 — 440	do.	Abundant in places	2.
Cayana	13.6	$\pm$ 644	do.	Scarce	4-6.
<i>Saccharum spontaneum</i>	12.5	$\pm$ 400	do.	Abundant	—
Chunnee	7.6	$\pm$ 504	do.	Absent	—

a. Covered by a 16-mm. objective and a No. X6 ocular, or an area of 2.4 sq. mm.

Beyond the epidermis there lies a narrow cortical zone consisting of small thin-walled parenchymatous cells passing insensibly into the parenchyma which

constitutes the filler between the bundles of the vascular tissue. Immediately below the epidermis, however, 2 to 4 rows of cells form a sclerenchymatous mantle, the individual cells there found being small, thick-walled and strongly lignified. Where stomata occur, this sclerenchyma is broken by loosely packed parenchyma.

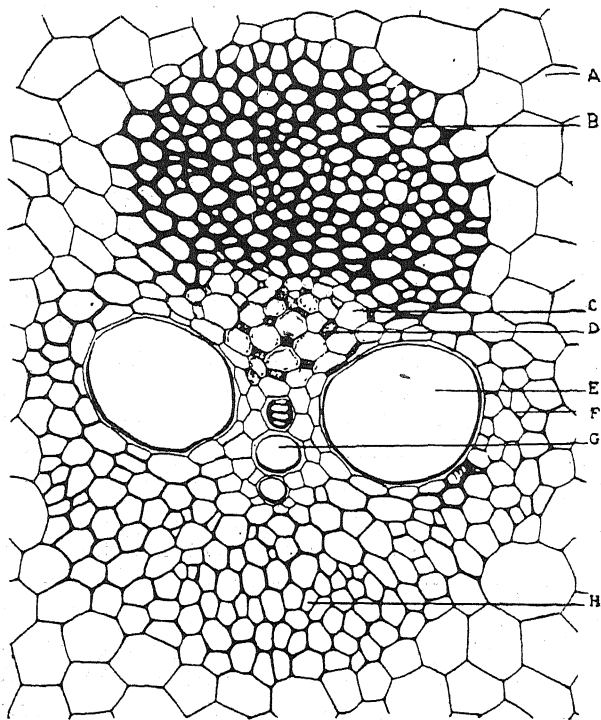


FIG. 123. Cross-section of large stem bundle. X 240.

A, Outer bundle parenchyma; B, sclerenchyma cap; C, sieve tube; D, companion cell; E, large pitted vessel; F, bundle sheath; G, protoxylem; H, sclerenchyma cap of xylem pole of bundle. (After Artschwager.)

The bundles are scattered somewhat irregularly throughout the massive central area. They increase in number from the centre towards the margin, at the same time decreasing in size. At the periphery they are small and so numerous as to form practically a continuous ring. Structurally these bundles of the periphery also show certain differences from the central bundle.

*Central Bundles.*—In cross-section, a typical bundle is rhomboidal in outline, surrounded by a sclerenchymatous sheath which to the interior and exterior enlarges to form a well-developed bundle cap. Xylem and phloem of each bundle are collaterally disposed. The proto-xylem consists of a few annular and spiral elements. Below the innermost elements, a well-developed lacuna may form, a lysigenous cavity into which the remnants of the first formed annular elements may project. Beyond and on either side of the proto-xylem a single large vessel is situated. These two large vessels are inter-connected by parenchyma interspersed by narrow vessels. Tangentially flattened parenchymatous cells, often

with reticulate thickenings and numerous pits, surround and inter-connect all the vessels.

The phloem lies behind the xylem, separated therefrom by a narrow zone of parenchyma. It consists of an oval mass of sieve tubes and their companion cells with the proto-phloem furthest to the exterior.

The bundle sheath forms a continuous layer of uninterrupted cells which are thick-walled, slightly pitted and elongated. Except at the junction of xylem and phloem where the cells are shorter and possess nearly transverse walls, their end walls are pointed. They are in direct contact with the proto-phloem but not in contact with the other phloem elements nor with any of the xylem elements.

*Peripheral Bundles.*—Towards the periphery of the stem the bundles are very numerous, oval in outline, becoming almost spherical in the outer ring. A massive development of sclerenchyma behind the xylem is characteristic. There is generally no proto-xylem lacuna; also the phloem is markedly reduced and more or less triangular in outline with the apex lying between the two large vessels. The bundles of the outermost ring lack both proto-phloem and proto-xylem and often consist mainly of sclerenchyma.

b. AT THE NODES.—Here a number of the central bundles branch or bend abruptly outwards. The parenchyma bordering the bundles enlarges radially, surrounding each bundle in a stellate manner. The sheath cells have lignified but thin walls. At the xylem pole the sclerenchyma practically disappears; at the phloem pole, the cap is greatly enlarged with the walls very thick and strongly lignified. Proto-xylem elements tend to increase, but there is no lacuna. The phloem as a whole also increases, but the individual elements tend to become lignified and non-functional.

The peripheral bundles at the node tend to break up into small bundles of varying shape, each irregular bundle surrounded by a stellate parenchyma.

c. ABOVE THE NODE.—1. *Keimring region.*—At the so-called “Keimring”, the cortex is more than doubled. The vascular bundles here change from the nodal condition to the inter-nodal condition:—the stellate parenchyma disappears; the phloem cap is reduced; the xylem cap reappears.

2. *Meristematic region.*—Here all the bundles show a marked loss of lignification, whilst the sclerenchymatous caps are transformed into collenchyma. The large peripheral bundles appear to increase in size, this increase being due to a huge collenchymatous jacket surrounding the reduced vascular centre. As a result the bundles are so crowded that the whole has a honeycomb appearance.

LEAF TRACES.—Except at the stem apex, the large number of traces entering a leaf and the complexity of the nodal structure render it impossible to follow the course of the bundles. At the apex, according to Artschwager (l.c.), the larger traces pass from the periphery of the stem to the centre and from there in a curve pass outwards into the leaf whose convex side is upwards. The intermediate-sized bundles sweep outwards more steeply; the small bundles seem to pass direct from the periphery. The large bundles may pass independently through about 8 inter-nodes; the intermediate pass through fewer nodes; the smallest terminate in the same inter-node. Further, all the bundles pursue, not a straight, but a spiral course, thus rendering it still more difficult to follow their entire length.

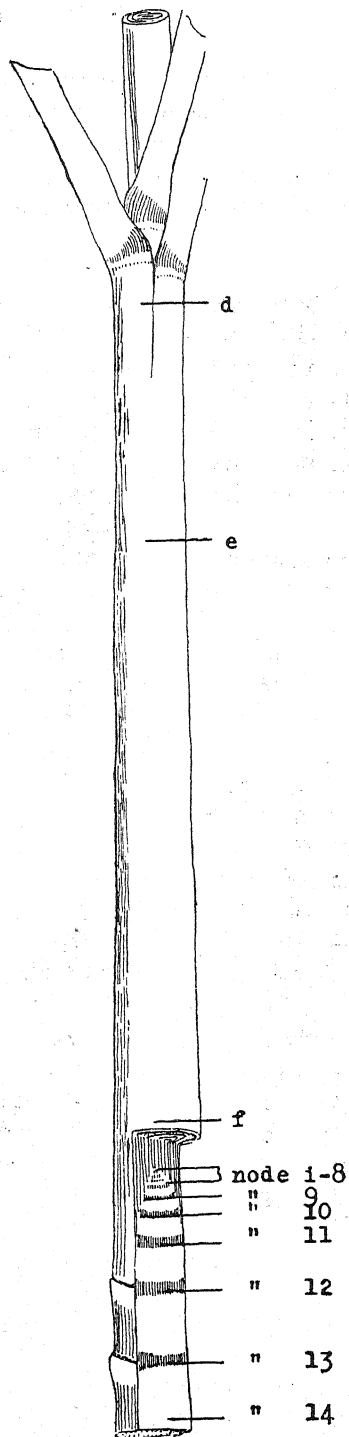


FIG. 124.

Upper part of sugar cane with leaves cut off and stem split open so as to expose the growing point and show its position in regard to the leaves. Nodes 14, 13 and 12 have leaf sheaths already mature, d indicates the position of the termination of the

LEAVES.—Each leaf exhibits the characteristic sheath and blade of the grass family. The sheath is inserted at the node and gradually narrows to its junction with the blade. At the base it is swollen to form a pseudo-joint; a somewhat similar joint is found at the junction with the blade. The margins of the sheath overlap and as the leaves are opposite and alternate, if the first sheath forms a

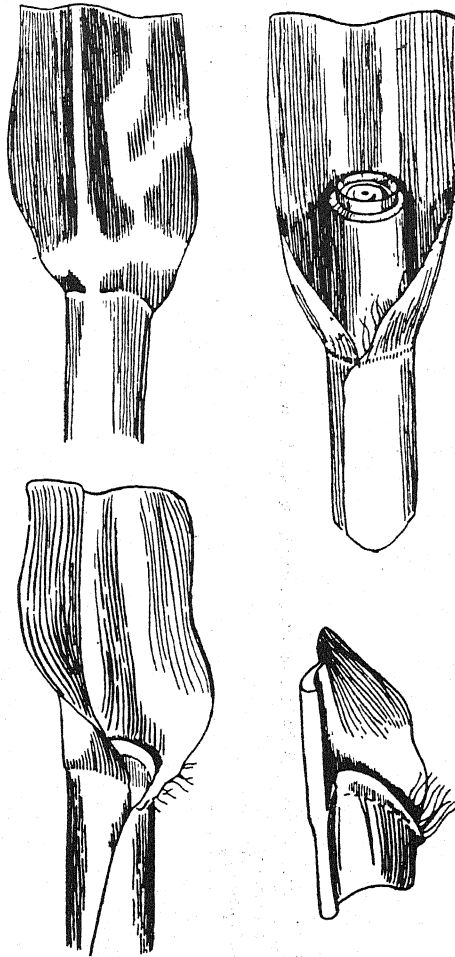


FIG. 125.

Four views of blade, joint and ligule. (After Artschwager.)

right-hand spiral, the next forms a left spiral. The surface of the sheath is covered with various hairs and at the base of the ligule, long silky cilia develop from the inner epidermis of the sheath.

LIGULE.—In the sugar cane the ligule is a fairly well-developed hyaline membrane. Its outer epidermis bears long hairs which are adnate to the surface, but become free at the apex to form a delicate fringe. On either side of the



base of the blade and close to the ligule, scarious extensions of the leaf sheath, known as the ligular processes, may occur.

**BLADE.**—The blade is linear, lanceolate in outline, reaching a length of 2 m., and a maximum diameter of 7 cm. The mid-rib is prominent, projecting from the lower surface and forming a groove on the upper. The margins are denticulate with fine silicified teeth; the surfaces hispid to pubescent, the longer and finer hairs being found on the lower face.

**ANATOMY OF THE SHEATH.**—The outer epidermis resembles the stem epidermis. The cells are thick-walled, pitted and undulated. Short cells are numerous, especially at the blade joint. There, and at the sheath joint, all the cells become thin-walled and somewhat irregular in shape. Stomata and hairs are numerous. The pubescence varies from numerous long delicate hairs at the joints to short strongly lignified ones interspersed with 2-celled appressed hairs, both somewhat sparsely distributed.

The cells of the inner epidermis are large and uniformly rectangular. Short cells are absent; hairs and stomata are few in number.

The interior of the sheath consists of radial rows of bundles embedded in parenchyma which shows a marked tendency to break down. The bundles tend to be arranged in an alternating series of large and small bundles. The large bundles are near to the centre of the sheath; the small bundles are close to or actually touch the epidermis. The large bundles are more or less similar to the stem bundles, but may consist of 2 or even 3 bundles superimposed. Each bundle is surrounded by a sclerenchymatous sheath with a well-developed outer cap. To the interior of each bundle, the parenchyma is prolonged more or less radially to end in a small mass of sclerenchyma separated from the inner epidermis by a single layer of parenchyma.

The base of the sheath is swollen and otherwise modified. All sclerenchymatous elements are transformed into collenchyma; the large air-spaces of the upper regions disappear, and are replaced by small closely-packed parenchyma; the bundles increase in number and are arranged in three more or less tangential bands. The innermost band is composed of large bundles widely spaced and often compound; the middle band consists of medium-sized bundles; the outermost band (next the outer epidermis) consists of the smaller bundles, here composed mainly of collenchyma.

When the lower leaves are shed they break away at the joints which may thus be looked upon as an abscission layer.

Towards the apex, the sheath becomes narrower and thicker. As a result the bundles become more and more crowded and at the same time move towards the centre. The air-cavities also disappear, whilst the sclerenchyma groups near the outer epidermis enlarge. The inner sclerenchyma groups also enlarge and ultimately form a tangential band, separated from the epidermis by several layers of parenchyma, not one layer.

At the joint the central area shows little modification. At the flanges, however, the lateral bundles are modified:—sclerenchyma becomes collenchyma, and spiral vessels only occur in the xylem.

In the ligule, the tissue is composed wholly of elongated thin-walled parenchyma with the epidermal cells of both surfaces suberized.

ANATOMY OF THE BLADE.—Three types of bundles occur in the blades :

- a. Large rhomboid bundles.
- b. Medium oval bundles.
- c. Small round bundles.

Medium and small bundles alternate, whilst the large bundles appear at wider intervals. Medium and large bundles are situated in the middle of the tissue, but the small bundles are close to the lower epidermis. At the mid-rib, however, all the bundles pass to the lower surface, whilst the upper groups of sclerenchyma unite to form a solid band.

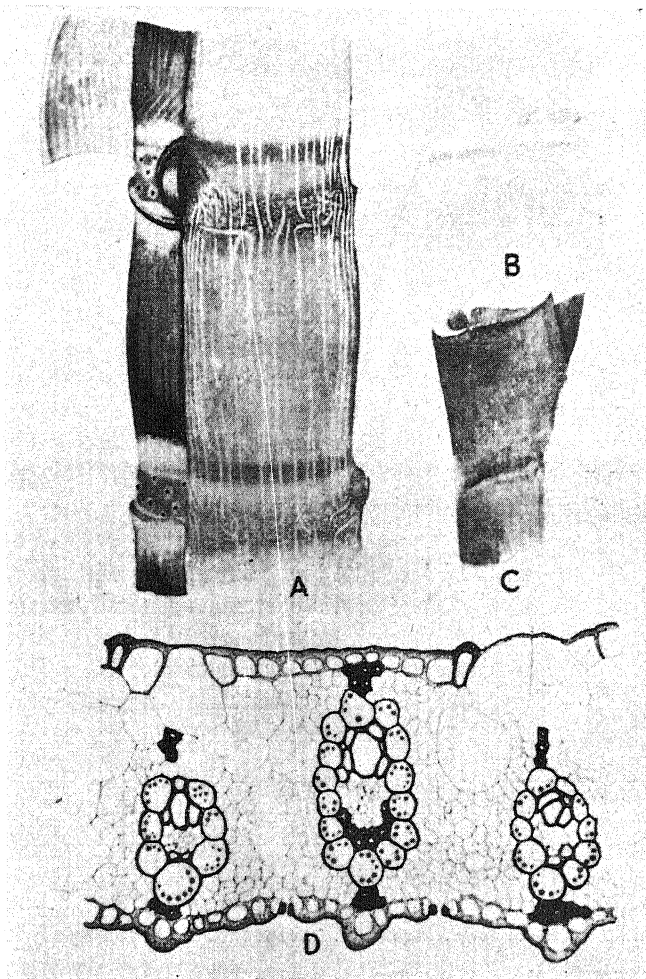


FIG. 126.

- A. Node and inter-node of mature stem.
- B. Base of leaf sheath.
- C. Blade joint ; the flanges of the joint brown and pubescent.
- D. Cross-section of mature leaf. X 200. (After Artschwager.—Original in colour.)

The larger bundles are girdered by sclerenchyma to both upper and lower surfaces. The small bundles are girdered only to the lower surfaces.

Each bundle is surrounded by a double sheath, the outer composed of large spherical cells containing chlorophyll (the chlorophyll sheath); the inner of fibres found mainly in the phloem regions. The chloroplasts of the sheath of all bundles are relatively large and few in number.

The xylem is well developed, and there is no lacuna except in the largest bundles.

The chlorophyll bearing leaf parenchyma forms a more or less concentric zone surrounding the bundles, except at the mid-rib where this parenchyma is found between the small bundles. The cells are in general small and irregular with numerous chloroplasts, smaller than those in the sheath, and apparently darker in colour. Adjacent to and more or less surrounding the chlorophyll parenchyma, are large colourless cells, with scanty protoplasm and watery sap. Interconnection between the bundles is effected by means of narrow branches which pass out either diagonally or at right angles. As the leaf narrows towards the apex, the bundles decrease in number. This is due either to fusion or to reduction, the bundles running out until there remains only a few phloem and xylem cells or finally elongated parenchyma.

The epidermal cells of both surfaces are brick-shaped with the longer diameter parallel to the leaf axis. The walls are thickened, lignified and undulated. Short cells, either occurring singly or in pairs, are fairly regularly interspersed. Between the larger bundles, longitudinal rows of the upper epidermal cells enlarge to form the so-called bulbiform cells or "motor cells". Their walls are thin, and they become progressively larger and then smaller. These cells are in contact with the large colourless parenchyma of the leaf.

Above the veins the epidermal cells are greatly elongated and very markedly thickened.

The stomata are situated in parallel rows, alternating with normal epidermal cells. Between two veins, three such rows of stomata generally occur on the lower surface; on the upper surface one row on each side of a large vein is the normal condition. The structure of the stomata is similar to that found in all gramineae. (Dickhoff, 1912; Kamerling, 1902; Geerts, 1916; Takenouchi, 1922; Artschwager, 1925.)

**INFLORESCENCE.**—The inflorescence is a loose terminal panicle—the so-called "arrow"—varying according to the variety in both size and shape. The main axis is long in *S. officinarum* and medium in *S. sinense* and short in *S. spontaneum*. At the base it is straight, thick and round; above it becomes thinner, sinuous and definitely grooved. The long hairs are absent and the axis may even be glabrate in *S. spontaneum*, *S. sinense* and *S. Barberi* Jeswiet; long hairs are always present in *S. officinarum*.

The main axis carries laterals of the first order. At the base they are long, far apart and arranged in semi-whorls; higher up they are shorter, closer together and arranged in whorls. All are triangular at the base with a cushion-like swelling at the joint and more or less rounded above. The laterals of the first order carry laterals of the second order and ultimately even of the third order, but the degree

of secondary branching decreases from the base upwards. These laterals of the second and third order are normally triangular in outline.

Ultimately a lateral, whether of the first, second or third order, bears one or more rachises. Each rachis is articulate and very brittle, the segments narrow at the base, broader at the apex, with one side more or less convex and the other flattened and slightly concave. At each node a rachis bears a pair of spikelets, one sessile, the other pedicelled.

The growing point of the axis differentiates into the initials of the panicle some three months before flowering takes place. In the interval, the panicle differentiates and is gradually carried upwards in a markedly contracted condition by the successive elongation of the inter-nodes. Further, the uppermost leaves, which envelop the panicle and are differentiated just prior to its formation, differ from the normal. Their sheaths as they develop become progressively longer whilst the blades remain relatively short. Indeed, the last leaf sheath at maturity may be a metre long, whilst the blade or "flag" is but a few decimetres. These leaves are sometimes spoken of as the "floral leaves" and may be 7 to 8 in number. In length their relative development may be taken as an index of the flowering period, and the sequence has been described by Wilbrink and Ledebøer (1911). Bremer (1923), adopting the method used by Kuyper (1915) in indicating the development of the shoot, has figured graphically the whole sequence of the development of the "floral leaves" and the panicle.

ANATOMY OF THE MAIN AXIS, LATERALS AND RACHIS.—Artschwager *et al.* (1929) have described the structure in detail.

The main axis has a similar anatomical structure to that of the stem. An epidermis of long narrow cells with sinuous walls alternating with short cells, invests the whole. A narrow cortex with thick-walled lignified cells follows. The interior is filled by a parenchymatous tissue, in which the vascular bundles are embedded. Towards the centre, however, the vascular bundles are absent and often the axis becomes hollow. The marginal bundles are so small and so numerous that they tend to form almost a solid ring. At the insertion of the laterals a cushion-like swelling, mainly consisting of parenchymatous cells, occurs. These cushions are responsible for the initial expansion of the laterals, and subsequently enable them to contract under unfavourable conditions.

The lateral axes possess a structure similar to, but simpler than, that of the main axis. The outermost bundles are numerous and small but the larger inner bundles become fewer in number.

The rachis carrying the spikelet normally contains five bundles. Three of the bundles are small and peripherally situated; two are large and more or less central. Just below the node these bundles divide into a number of traces which supply the vascular system of the sessile spikelet, the pedicel of the stalked spikelet and ultimately the stalked spikelet itself.

Of the large bundles, bundle A divides into three parts:—Strand A<sup>1</sup> passes into the pedicel; Strands A<sup>2</sup> and A<sup>3</sup> run more or less parallel to one another through the node, and thereafter reunite to reconstitute A. The second bundle B divides into two, B<sup>1</sup> and B<sup>2</sup>. B<sup>1</sup> passes up the rachis to reconstitute the second large bundle of the next inter-node; B<sup>2</sup> passes outwards into the base of the sessile spikelet, there dividing to form the larger part of its vascular system. Of the

three small bundles, C divides and both strands pass through the node to form two of the small bundles of the next inter-node ; D also divides, one strand passing directly into the pedicel, the other re-dividing and sending one strand into the pedicel, the other into the sessile spikelet. E divides, the one branch entering the sessile spikelet, the other passing up the node to form the third small bundle of the next inter-node.

**THE SPIKELETS.**—As we have seen, there are 2 spikelets at each node, one sessile and one pedicelled. Each spikelet is surrounded by a row of long hairs, is oblong lanceolate in outline and contains 2 flowers, the lower sterile the upper hermaphrodite.

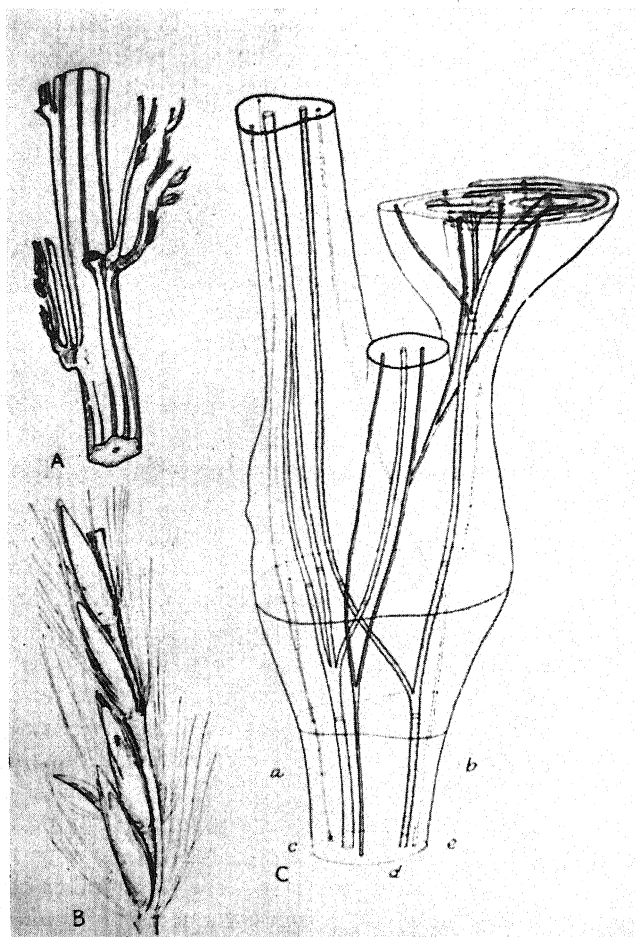


FIG. 127. Main axis and laterals of inflorescence.

- A. Lateral axes arising from same cushion joint of upper part of main axis.
- B. Part of rachis of inflorescence. Each articulation carries 2 spikelets, 1 sessile, the other pedicelled.
- C. Diagram of the course of the vascular system of the rachis, the pedicel and the sessile spikelet ; *a* and *b* represent the 2 large bundles of the rachis ; *c*, *d* and *e*, the 3 small peripheral bundles. (After Artschwager.)

The outer glume is lanceolate, bicarinate, with the upper two-thirds shortly hairy, especially on the keels and the upper margins, and fringed with long unicellular hairs; the inner glume is similar, but has a distinct mid-rib and longer hairs along the margin. The sterile flower is represented by the lemma, which is shorter than the inner glume, more delicate than either and usually without vascular tissue. The tip may be blunt or pointed and the edges carry long hairs. All other structures are wanting.

The fertile flower may or may not possess a lemma. When present, as in

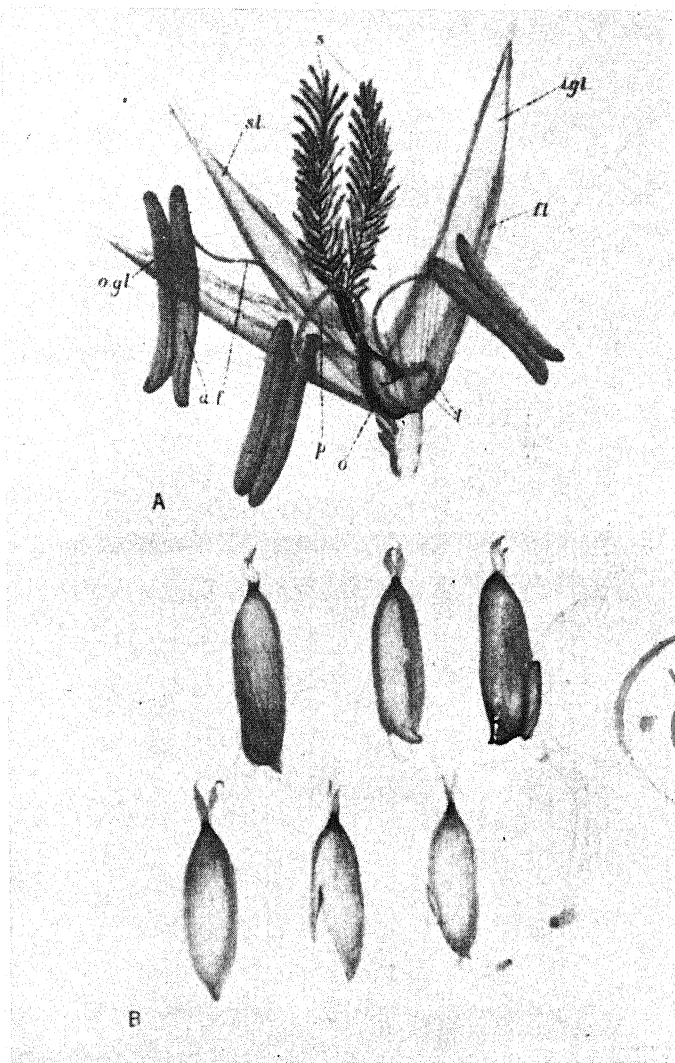
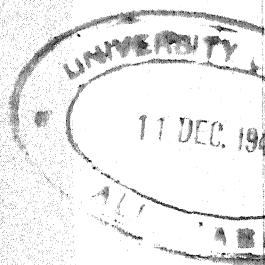


FIG. 128. Spikelet of Cane. U.S. 759.

*o.gl*, Outer glume; *i.gl*, inner glume; *s.l*, sterile lemma; *f.l*, fertile lemma (absent in certain types); *p*, palea; *l*, lodicules; *o*, ovary; *s*, stigma; *a*, anther; *f*, filament of anther. X 12. (After Artschwager.—Original in colour.)



*S. spontaneum*, *S. sinense*, *S. Barberi* and certain forms of *S. officinarum*, it is a narrow non-vascular scale, tipped with fine hairs. The palea is always small and according to Wilbrink and Jeswiet, differs in shape and pubescence in different forms. It is strongly invested by the lemma of the sterile flower. Opposite the palea there are 2 lodicules, short and wedge-shaped and strongly ciliate in certain forms. There are 3 stamens, one inserted between the lodicules, the other two on the opposite side. The filaments are white and round, at first short, then elongating rapidly. The anthers are bilobed and versatile, at first yellow, then purple. The ovary is obovate to obconical, round but somewhat flattened on the ventral side. It carries two terminal styles, each ending in feathery stigmas which are purplish in colour. The single ascending anatropous ovule is attached to the inner ventral surface of the ovary by a broad placenta.

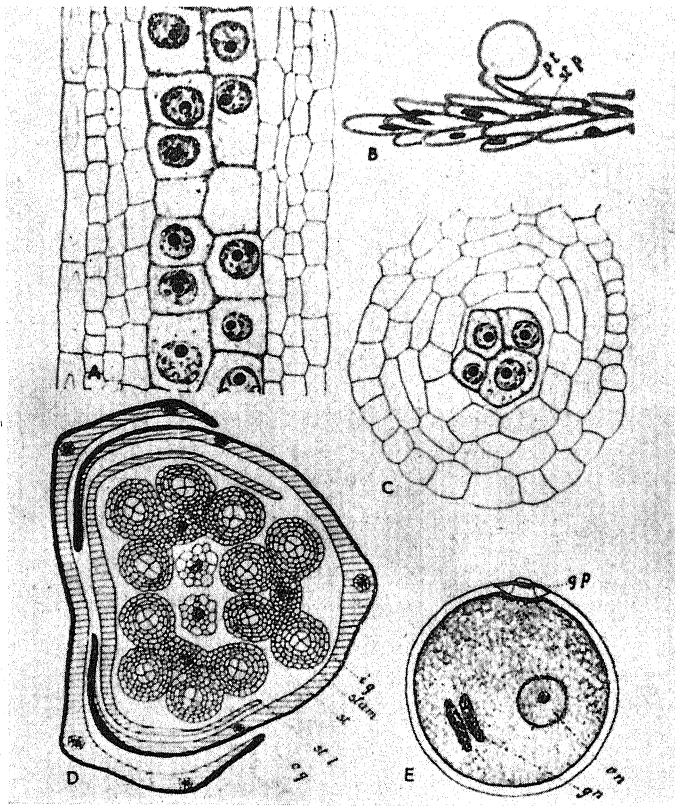


FIG. 129.

- A. Longitudinal section of an anther with pollen in mother-cell stage. X 820.
- B. Lateral branch of feathery stigma with germinating pollen grain. X 200. *pt*, Pollen tube; *st.p*, stigmatic papilla.
- C. Cross-section of anther with pollen in mother-cell stage. X 560.
- D. Cross-section of young floret; *o.g*, outer glume; *i.g*, inner glume; *st.l*, lemma of infertile flower; *stam*, stamen; *st*, style.
- E. Mature pollen grain. X 900. *v.n*, vegetative nucleus; *g.n*, generative nuclei; *g.p*, germ pore. (After Artschwager.)

## DEVELOPMENT OF THE SPIKELET AND GAMETOGENESIS.—

The pedicelled spikelet commences to develop before the sessile one. A general account is given by Artschwager *et al.* (1929), and appears to correspond very closely to that found in grasses generally and the account here given for maize (pages 411-412).

Each anther lobe contains 2 loculi, united at maturity owing to the breaking down of the intervening tissue. In each loculus the pollen mother cells form two regular longitudinal rows, bordered by tapetal cells; in cross-section they form a group of 4 cells, each cell on its outer surface in contact with a tapetal cell. Meiosis is said to commence when the panicle is just about to flag. In any one flower the divisions may be more or less simultaneous or may exhibit different

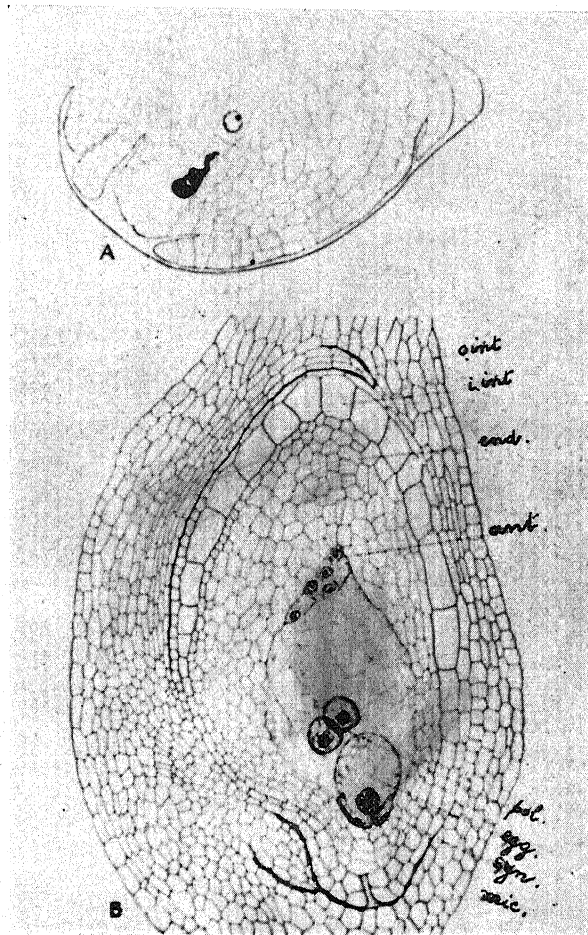


FIG. 130. Embryo-sac.

- A. Ovule with row of 4 megaspores of which 3 are degenerating. X 200.  
 B. Ovule with 8-celled embryo-sac, X 200. *o.int*, Outer integument; *i.int*, inner integument; *end*, nucellus; *ant*, antipodals; *pol*, polar nuclei; *egg*, egg; *syn*, synergidae; *mic*, micropyle. (After Artschwager.)



stages. Also, the divisions are found first on the flowers at the top of the main axis and at the tips of the laterals, progressing thereafterwards downwards and centripetally. The interval between the appearance of the mother cells at the top and at the base is said to be 6 days in *S. officinarum*; only 4 days in *S. spontaneum* (Bremer, 1923). Bremer (1923-31) and Artschwager *et al.* (1929) have given a general description of the divisions. Artschwager in his material found the haploid chromosome numbers to be 58 in U.S. 875 (Kassoer seedling), and in U.S. 1794 (a P.O.J. seedling) to be 40. These numbers correspond to those found

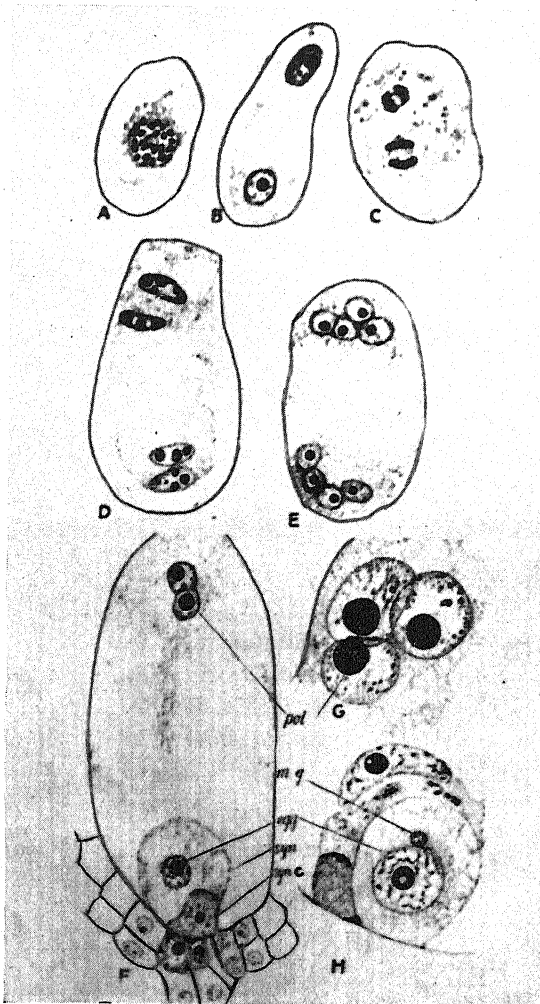


FIG. 131. Stages in the development of the Embryo-sac.

A to E. Stages from 1 to 8 nucleate condition. X 480.

F. Embryo-sac with polar nuclei far removed from egg. X 240.

G. Group of 3 polar nuclei. X 500.

H. Fertilization of egg; *syn.c*, synergidae cap; *m.g*, male gamete. X 500. (After Artschwager.)

by Bremer in his extensive study of the chromosomes of a large number of types (page 349).

Artschwager *et al.* (l.c.) also studied the developmental sequence in the ovule and the embryo-sac, whilst other investigators have given partial details.

The young ovule is a hemispherical mass of parenchymatous tissue. As it enlarges it curves and becomes anatropous, and at the same time is gradually invested by two integuments. The outer is never complete and later disintegrates; the inner is complete and ultimately forms the testa. Each consists of a double row of cells, except at the placenta and the micropyle where three to four layers (Guerin, 1899) are found.

The archesporium is a large wedge-shaped sub-epidermal cell easily recognizable at the time when the integuments appear. It enlarges until the integuments are fully developed; then it divides twice in succession to form a row of 4 megaspores. The three outer disintegrate; the innermost is functional and enlarges to form the embryo-sac.

The development of the embryo-sac follows the usual course (cp. wheat and maize). A number of antipodal cells form, binucleate or multinucleate, but they degenerate prior to fertilization. At maturity the 2 polar nuclei are distinct and close to the egg: the synergidae are distinct but their nuclei are inconspicuous. The egg is large, situated immediately above the synergidae and has a conspicuous nucleus.

The nucellar tissue remains fairly massive especially at the antipodal end; the inner integument is distinct, with the cells of the inner layer in contact with the nucellus and much enlarged; the outer integument is markedly incomplete.

**ANTHESIS AND POLLINATION.**—The detail of flower opening has been followed by several investigators, more especially by Brandes, Mameli de Calvino (1925), Barnum and McIntosh (1930). In general anthesis is downward and centripetal. Flowers open during the night or very early morning. The first indication is the protrusion of the stigmas, followed by the falling apart of the glumes. Some three hours later the anthers commence to dehisce. According to McIntosh (l.c.) dehiscence begins about 3 a.m. and ends about 10 a.m. Before and after these periods there is little or no dehiscence. Within the period there is for each variety a variable period of maximum dehiscence, generally between 6 a.m. and 8.30 a.m. There is, however, seasonal variation and variation from locality to locality. The chief environmental factors appear to be temperature and moisture, though McIntosh is of the opinion that evaporation as such may prove to be more significant than either.

Further, the varieties themselves vary markedly in their capacity to produce pollen, ranging from the abundant pollen production of *S. spontaneum* to forms which produce little or no pollen. This variability is an inherent characteristic.

Some difficulty has been encountered in germinating cane pollen. Venkatraman (1922), after testing the live stigma of a number of plants, finally selected the stigmas of *Datura fastuosa* v. *alba* for all viability trials. In a similar manner, Cottrell-Dormer (1924) and Mercado (1926) have employed sugar cane stigmas themselves. Dutt and Ayyar (1926) then succeeded in germinating the pollen on media consisting of 26 per cent. sucrose plus 0.7 per cent. agar. The germination of a number of types was tested on these media, the percentage obtained

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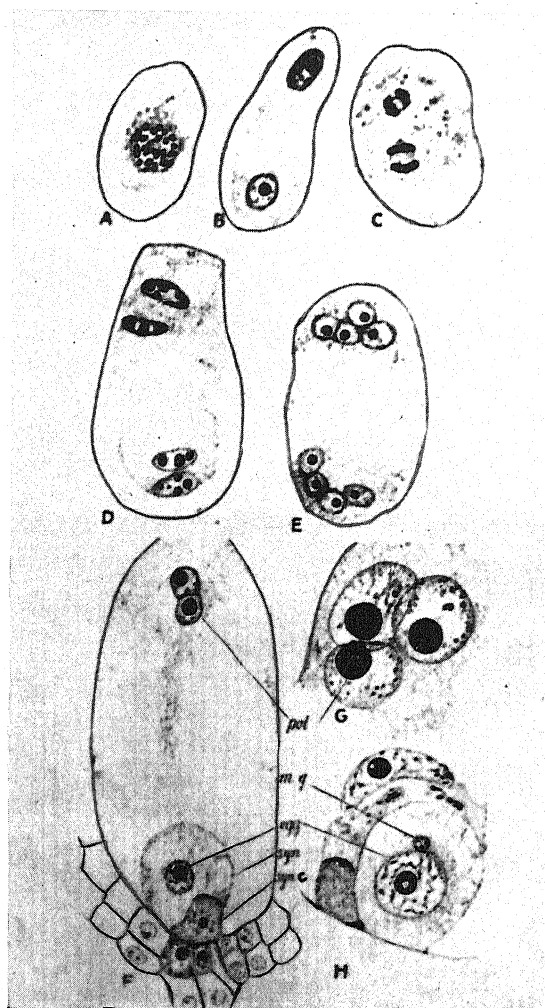


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ranging from 3 to 61. A temperature range from 22° C. to 33° C. gave satisfactory results, but a tendency to burst was found at higher temperatures. In Java the iodine test for pollen viability has been in general practice, but the method is not regarded as altogether satisfactory.

Under normal conditions, cane pollen retains its viability for only a brief period (1 to 2 hours). This loss of viability has led to difficulties in securing certain crossings and, as a consequence, attempts have been made to check the deterioration of the pollen. Venkatraman (1922) found that if the arrows are cut when the first anthers are ready to dehisce and stored under moist conditions, viable pollen may be obtained from such arrows over a period of 10 days. Verret (1925) also found that cut arrows placed in a solution of 1 : 2,000 sulphurous acid could live for several weeks, and that pollen from such arrows was viable 10 days after cutting. Venkatraman (1926) then devised a method of identifying a cane about to arrow, surrounding it with a tile pot and after it had produced adventitious roots, cutting it off below the pot. In this way the arrowing cane can be removed and used as desired. Finally, Dutt (1929) discovered that pollen stored in an atmosphere of  $\text{CO}_2$  with a relative humidity of 85 per cent. and a temperature of from 5° to 13° C., could retain its vitality for 12 days; and Weller (1926) found that a pH of 5.2, a humidity of 96 per cent. and a temperature of 23° C. were optimum for artificial germination on media.

Not only is there variability in pollen sterility, but there may be sterility in the ovules. To what extent this occurs is as yet uncertain.

**FERTILIZATION.**—Under normal conditions, the pollen on the stigmatic papillae germinates immediately. The tube enters a stigmatic branch and grows down the conductive tissue of the style. On entering the ovary, it grows downwards to the micropyle, thence between the cells of the nucellus to the egg. In Hawaii, Mangelsdorf and Lennox have found varieties which are self-incompatible.

**DEVELOPMENT OF EMBRYO AND CARYOPSIS.**—According to Artschwager *et al.* (1929) the development of the embryo appears to be similar to that found in other grasses (see wheat, pages 115-116). The endosperm is derived from the 2 polar nuclei plus the second male nucleus. They fuse at or just after the time of fertilization and commence to divide immediately. Soon the resulting nuclei are to be found irregularly scattered in the lining cytoplasm. As they increase in number they are enclosed in protoplasm and finally separated by walls. Thereafter their growth is rapid, filling the embryo-sac and replacing the nucellus.

**THE SEED.**—Cane sugar seed is, considering the ultimate size of the plant, excessively minute. The average length is approximately 1.5 mm. and the maximum width .5 mm. It is yellowish-brown in colour, ovate to oblong in shape, with a minute scar at the proximal end and frequently the remains of the style at the distal. A slight depression may mark the position of the embryo, which is relatively large in comparison with the size of the endosperm. Cobb (1905), Barber (1916) and Artschwager *et al.* (1929) have described the structure.

**PERICARP.**—An outer epidermis of rectilinear and relatively thin-walled cells invests the whole. The middle region consists of somewhat irregular thin-walled cells showing no marked differentiation. The inner epidermis, in contact

with the testa, forms a single layer of thin-walled tubular cells, circular to broadly elliptical in cross-section.

TESTA.—This is a single layer, the product of the inner integument. The cells are large, rectangular in outline with yellowish-brown walls and homogeneous content. Over the embryo the testa is thinner and lighter in colour ; at the distal end its cells are larger.

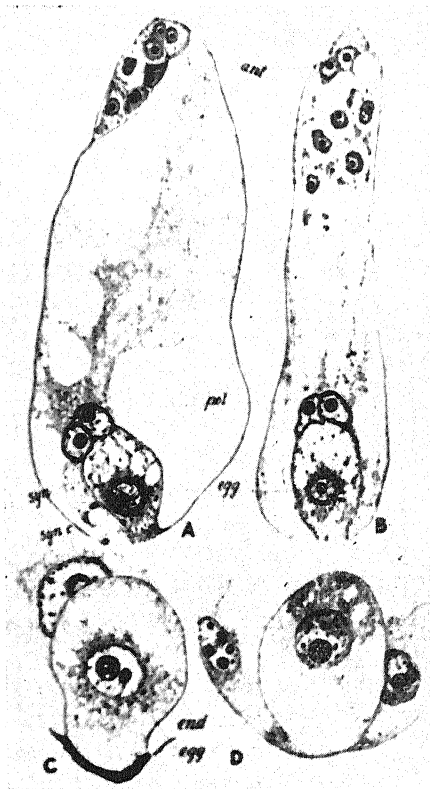


FIG. 132. Fertilization.

- A. Longitudinal sagittal section of embryo-sac ; *ant*, antipodals ; *pol*, polar nuclei ; *syn*, synergidae ; *syn.c*, synergidal cap. X 175.
- B. Longitudinal radial section of embryo-sac. X 175.
- C. Egg nucleus with 2 nucleoli. X 430.
- D. Fertilized egg surrounded by free endosperm (*en*) nuclei. X 430. (After Artschwager.)

ENDOSPERM.—The endosperm mass consists of thin-walled polyhedral cells containing starch granules. Its outermost layer in contact with the testa differentiates as an aleurone. The cells of this aleurone are polygonal in surface view, rectangular in cross-section. They contain an oval nucleus, several nucleoli and spherical aleurone grains embedded in an oily cytoplasm.

EMBRYO.—The embryo is somewhat similar to that of the wheat plant. The scutellum is massive, convex in longitudinal section, somewhat flattened in

transverse section, and invests the remainder of the embryo in a manner similar to but less marked than that found in maize. The mesocotyl is short and carries the plumule, which is completely invested by the coleoptile. Within the coleoptile there are a number of rudimentary leaves surrounding the growing point. The radicle is short and broad with a distinct root cap, and invested by the coleorhiza. There is no epiblast.

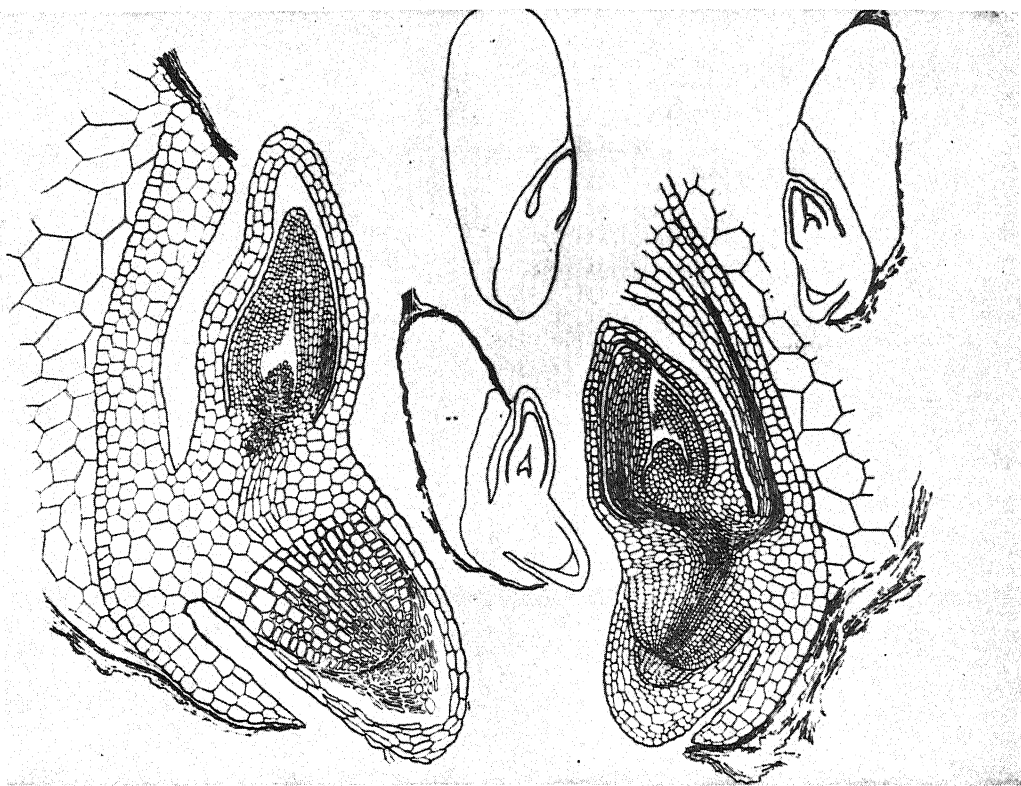


FIG. 133.

Longitudinal sections of embryo, showing its position in relation to the caryopsis. Note the absence of epiblast. (After Barber.)

**GERMINATION.**—Cane sugar seed has poor keeping qualities. In spite of its smallness it seems to germinate better in full sunlight than in shade. Under favourable conditions, the coleorhiza ruptures the base in approximately 24 hours. Thereafter the primary root emerges, grows for a few millimetres, and is replaced by a secondary root. The plumule emerges almost immediately after. When the coleoptile appears above ground level, its apex ruptures and the first leaf emerges. The first adventitious roots then develop near the ground level. The development of the seedling is rapid. At 4 months old a number of tillers may be well developed. It does not, however, attain maturity until about 18 months old. (Barber, 1916; Artschwager, 1929.)

CYTOLOGY OF SUGAR CANE.—Franck (1911) first reported the chromosome number in *S. officinarum* to be 14 and 28. Kuwada (1915) then stated that the diploid number was 68, and ca 68 in *S. spontaneum*. Bremer (1923-34) thereafter published a series of papers in which the species and varieties were studied in detail.

TABLE XXXI.

CHROMOSOME NUMBERS OF SOME SACCHARUM SPECIES AND VARIETIES.  
(After Bremer.)

TYPE.	n.	2n.
<i>S. spontaneum</i> (ex Bornea) .. .. .	30	60
(?) .. .. .	36	72
"    "    (Glagah Tabongo of Celebes) .. .. .	40	80
(certain forms ex Celebes) .. .. .	48	96
(Glagah of Java and others) .. .. .	56	112
<i>S. sinense</i> (including Uba and Kavangire) .. .. .	ca 58	118
<i>S. officinarum</i> (many varieties, including Batjan) (Ardjoeno, Black Cheribon, etc.) .. .. .	40	80
<i>S. officinarum</i> var. Loethers .. .. .	ca 50	98-99
"    "    var. "Kassoer" .. .. .	68	136
"    "    var. "Toledo" .. .. .	68	136
<i>S. officinarum</i> × <i>S. spontaneum</i> of Java (n = 56) .. .. .	68	
<i>S. officinarum</i> × <i>S. spontaneum</i> of Celebes (n = 40) .. .. .	120/2	
P.O.J. 100 .. .. .	89/2	
P.O.J. 2354 .. .. .	157/2	
P.O.J. 2883 .. .. .	115/2	
<i>S. Barberi</i> Jeswiet		
Sunnabile Group Rahrara (Coimbatore), Rakhara Shahgahanpore, Dhambu .. .. .		82
Naanal, Khadya, Bransa 1 Sunnabile .. .. .		118
Mungo Group (9 varieties) .. .. .		82
Nargori Group Katai, Sararo, Hatheoni and Baruk .. .. .		124
Manga and Kewali .. .. .		107
Saretha Group (7 varieties) .. .. .		89-91

In these results it should be noted that each so-called species has a definite chromosome number. Within each species, however, abnormal numbers may occur, indicating either the existence of hybridity or the fact that the species itself is a complex.

Thus, there is now little doubt that *S. spontaneum* is a complex, since Bremer has found a series ranging from 60 to 72, 80, 96 and 112 (diploid chromosome numbers). In India, Dutt and Rao (1932) reported that the Coimbatore form had 64 chromosomes, whilst Singh (1934) found 54 in the Dehra Dun form; 34 in Rella Gadi, Godavery; 78 in the Dacca form; 108 in a thick-stemmed Sumatra form and 128 in a second similar Sumatra form. These numbers do not conform with Bremer's and may indicate either hybridity or a still greater nexus of forms. That the latter situation exists is evident from the morphological study of the species.



Both *Sinense* and *officinarum* (apart from hybrid forms) constitute definite types. The forms of *S. Barberi*, however, are obviously a complex. Bremer's recent analysis indicates that Barber's original group constitutes fairly definite chromosomal types, the variability found being probably due to hybridity; e.g., the varieties Manga and Kewali— $2n = 107$ —of the Nargori group are probably hybrids between members of the Nargori and Saretha groups. (62 + 45.)

Bremer is of the opinion that the basic chromosome number is 10, thus corresponding to that of the Andropogoneae. Singh (1934), however, suggests that the series indicate 8 as the possible basic number.

Certain forms of cane whose specific affinities were doubtful have, indeed, been proved to be hybrid. Thus, the variety "Kassoer" has 136 chromosomes, the complex found being similar to that present in the cross Black Cheribon  $\times$  *S. spontaneum* of Java.

It is indeed likely that Kassoer resulted from a natural cross of these types. The combination Black Cheribon  $\times$  *S. spontaneum*, however, would be expected to give a chromosome number of 96 (40 + 56). Bremer interprets the chromosome number obtained as a combination of the diploid number of the *S. officinarum* parent, viz. 80, plus the haploid number of *S. spontaneum*, i.e., 56. Similarly the hybrid of Black Cheribon  $\times$  *S. spontaneum* of Celebes would be a combination of the 80 diploid chromosomes of Black Cheribon with the 40 haploid chromosomes of this particular form of *S. spontaneum*. Support is given to this hypothesis by the fact that the Philippine cane Toledo, believed to be a natural hybrid, was found to have 120 chromosomes (i.e., 80 + 40). The position found in various other hybrids (P.O.J. series) suggests that this duplication of the chromosomes of the *S. officinarum* parent may occur with considerable regularity. At what period the duplication of the chromosomes of the *S. officinarum* parent takes place, however, has not definitely been established. The evidence indicates that reduction of the embryo-sac mother cell occurs, as the seedlings show marked segregation. Bremer is of the opinion that the reduction division does take place, and that during fertilization the *S. officinarum* chromosomes undergo longitudinal fission whilst the *S. spontaneum* chromosomes remain unsplit. It should also be noted that several other instances of duplication of the chromosomes of the seed parent in other plant species have been reported.

**HYBRIDIZATION STUDIES.**—The cane sugar plant is normally propagated by cuttings, and this method must have been employed for very many generations. During this long period, however, natural crossing must have taken place frequently, and unconscious selection of the hybrids so produced and subsequent vegetative propagation have resulted in the existence of many forms, all of which are heterozygous.

Until recently, propagation by seed was never practised, and at the present time is employed only for the breeding of new varieties. Indeed, the very existence of the seed was denied until recently. "Cariops in nemo adhuc videsse videtur" was written by Hackel in 1889! Nevertheless, the production of cane from seed had been reported both from Barbados and Java nearly 30 years before Hackel made his emphatic statement.

The first authentic cases of the raising of sugar cane from seed were those of Soltwedel in 1885, and of Harrison and Bowell (1889) independently in Barbados.

The caryopses as such were first described by Benecke (1889). Since then seedling canes have been raised in great numbers, and many hybrids have been produced, especially in Barbados, India, Hawaii and Java.

The earlier hybridization work undertaken was purely practical, directed to obtain high-yielding strains adapted to particular conditions and at the same time resistant to certain diseases such as the Sereh disease in Java. In India, the local canes, believed by Barber to be derived from *S. spontaneum*, have been crossed *inter se* and with the wild *S. spontaneum*. Crosses of *S. spontaneum* with the so-called Noble canes, *S. officinarum*, have also been obtained. Many of these Coimbatore hybrids, known as the Co series, such as Co 203, 205, 210, and 214 have become widely known. They have been described by Venkatraman (1928).



FIG. 134.

The cross P. O. J. 2725 sugar cane  $\times$  Texas Seeded Ribbon sorgo in bloom. (After Bourne.)

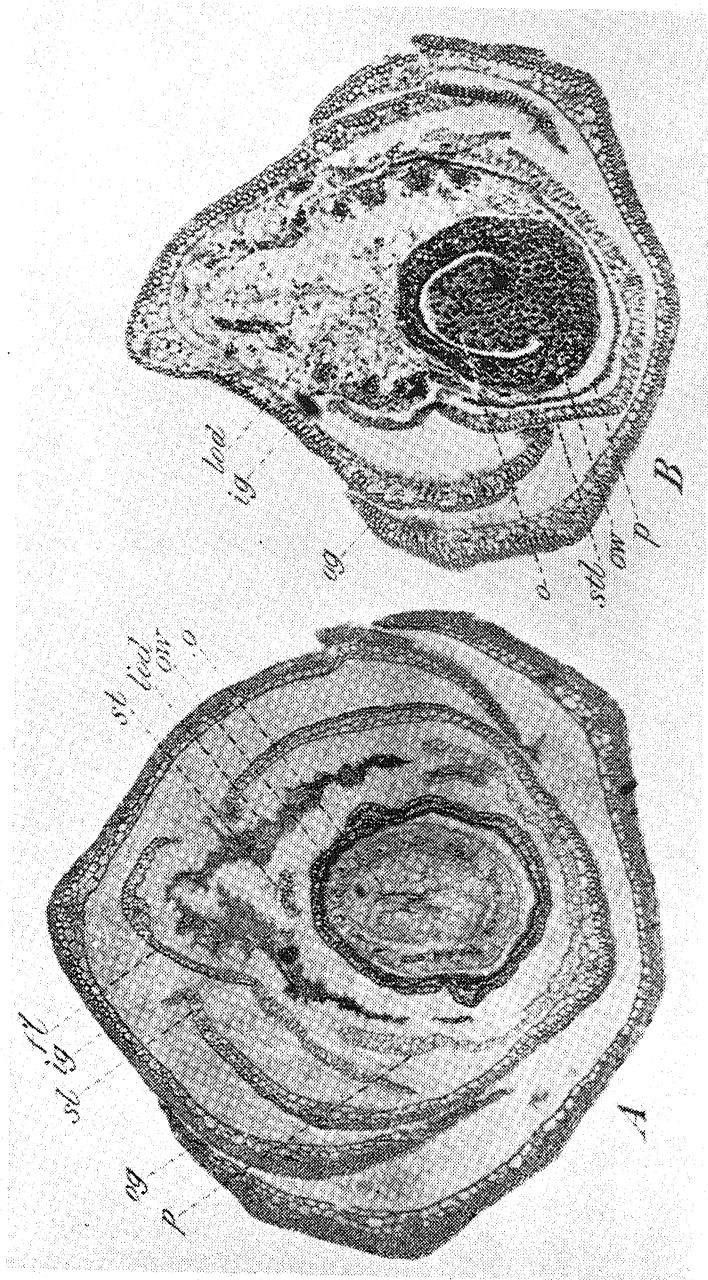


FIG. 135.

Sugar-Cane Sorghum Hybrids. *A*, Cross-section of normal spikelet of the hybrid F. 31-13, showing: *fl*, Fertile lemma; *ig*, inner glume; *sl*, sterile lemma; *og*, outer glume; *p*, palea; *lod*, lodicule; *ow*, ovary wall with 2 vascular strands; *o*, ovule, and *st*, stamen. X 105. *B*, Cross-section of spikelet of P. O. J. 2725 sugar cane, showing: *lod*, Lodicule; *ig*, inner glume; *og*, outer glume; *o*, ovule; *ow*, ovary wall; *sl*, sterile lemma, and *p*, palea. X 105. Note the greater diameter of the sugar cane × sorgho hybrid spikelet as compared with that of sugar cane. (After Bourne.)

In Java, the local canes were first inter-crossed and the resultant seedlings rigorously selected. Later, certain Indian varieties, such as "Chunnee" and "Ruckee" were crossed with the local canes. The resultant hybrids constituted the first of the P.O.J. series. Still later, as a result of the study of the hybrid cane, "Kassoer," the thick-stemmed Noble canes were inter-crossed with the local *S. spontaneum*, and a further series of P.O.J. canes obtained. This process of "ennobling" the thin canes with the constitution of the thick Noble canes has since been practised very extensively. Up to the present a vast series of combinations and re-combinations have been effected (see Kobus, 1893, Bannier, 1926). Hybridization work along somewhat similar lines is now being conducted both in Barbados and Hawaii.

In the production of these crosses, many practical difficulties have been encountered. The simplest method of securing a cross is to enclose the arrows of both parents in one cage. To secure this the parental plants must be grown alongside of one another, and must flower more or less simultaneously. With many types this is impossible. Further, the pollen is viable, under ordinary conditions, for only a short period, and many varieties produce little or no pollen. As a consequence the flowering habits of the varieties had to be studied, and methods secured of prolonging the life of the pollen. These methods have already been described. By altering the climatic condition, more especially by growing them at different altitudes, the varieties may be induced to flower at different but definite periods, and where necessary the pollen "arrow" may be brought from one district to that in which the future "seed parent" is growing. In Java, especially, it is possible to grow the canes at different altitudes within short distances and full advantage of this possibility has there been taken.

The process of "ennobling" has recently been advanced in a very striking manner. Thomas and Venkatraman (1928) succeeded in hybridizing P.O.J. 2725 (a *S. officinarum* hybrid) with the Durra form of Sorghum "periamanjai". The resulting hybrids were very varied in vigour and habit. A large number indeed were worthless, including a few albinos and many which exhibited poor root development.

All exhibited characteristics of both parents, but the few desirable economic types tended to resemble the sugar cane parent. Some of these were early maturing and gave satisfactory sugar yields when six months old (Venkatraman and Thomas, 1932). The results of more extended tests have since been published (Nath, *et al.*, 1932). The early crop (March planted) matured in 10 months; the June planted crop matured in 8 to 9 months. Compared with other sugar cane varieties, the hybrids tended to come to maturity a little earlier, and at the time of their maximum efficiency were decidedly richer. It would appear "that certain of these hybrids are capable of attaining a purity of 85 and over in about 200 to 220 days from the time of planting, and tend to improve in quality for nearly 100 days afterwards."

Bourne (1935) has also obtained similar hybrids and compared the hybrids morphologically with the parental species.

Singh (1934) studied the cytology of the hybrids. Eighty-five bivalents were found, and marked irregularity was noted. Since the *Saccharum* parent (P.O.J. 2725) possessed 106 somatic chromosomes (Bremer, 1928) and the *Sorghum* parent 20,

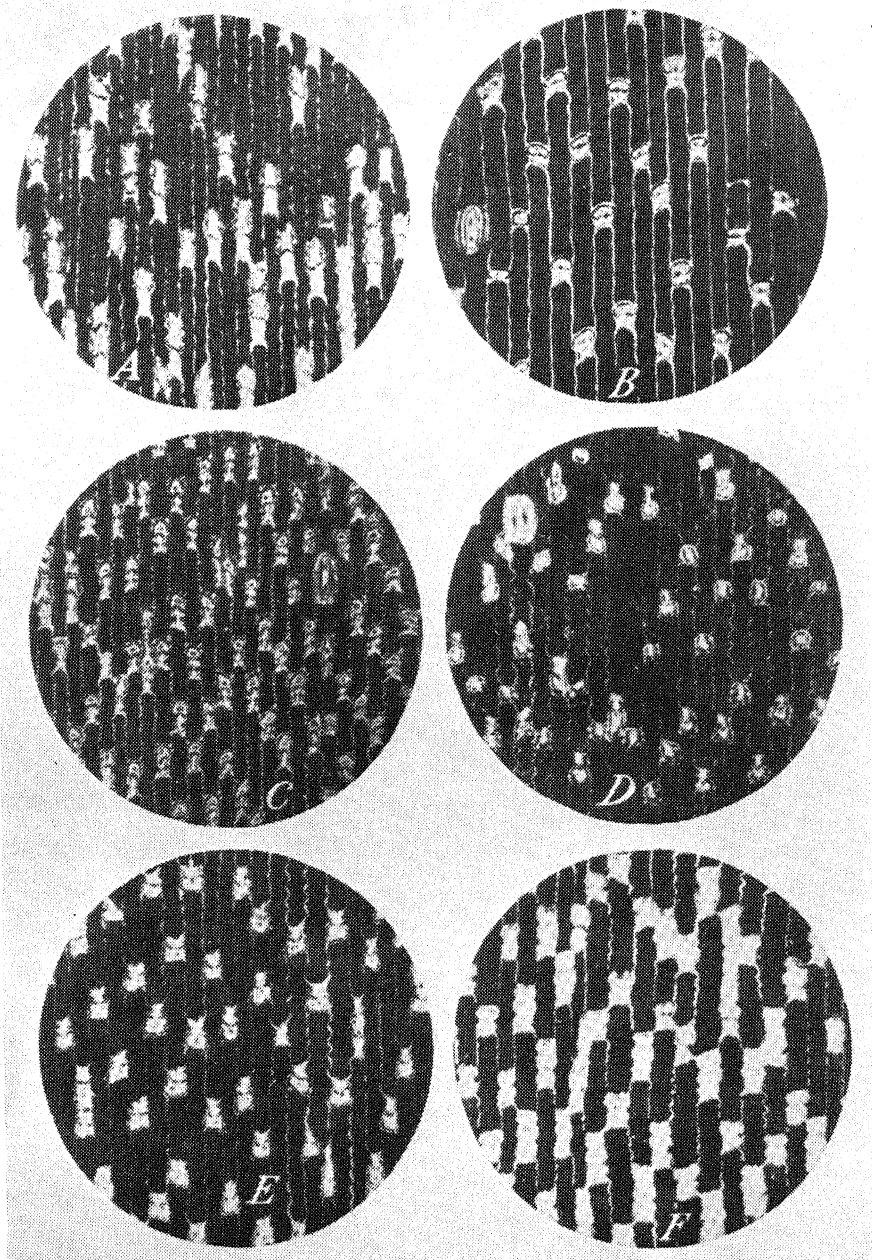


FIG. 136.

Anatomical structure of epidermis of stems of sugar cane, sorgho, and several hybrids between the two parental types: *A*, P. O. J. 2725 sugar cane; *B*, Texas Seeded Ribbon sorgho; *C*, hybrid F. 31-29; *D*, hybrid F. 31-33 (note frequent occurrence of solitary cork cells); *E*, hybrid F. 31-13; *F*, hybrid F. 31-6. All X 214. (After Bourne.)

it would appear that here also there has been a doubling of the chromosomes on the part of the sugar cane parent :— $\frac{(53-54) + (53-54) + 10}{2} \times 2 = 116-118$ .

In a further paper, Singh (1934) studied hybrids which showed more marked resemblance to the Sorghum parent than did the previous ones examined. Here the chromosome numbers were only  $\frac{53-54 + 10}{2} \times 2 = 63-64 (2n)$ . It would, therefore, appear that in the F<sub>1</sub> hybrids, types occur in which both doubling and non-doubling of the chromosome complement of the sugar cane parent has taken place.

In Java, attempts were made to cross *Saccharum spontaneum* and *Erianthus arundinaceus* as early as 1886. The seedlings, whether true hybrids or not, were apparently lost. In 1927, simultaneous flowering of *S. officinarum* (Clone E. K. 28) and certain *Erianthus* species, was taken advantage of, and as a result 10 hybrids were obtained with *Erianthus sara*. In the following year 300 hybrids were obtained. In every instance the cross was successful only when sugar cane was employed as the seed parent. No hybrids were obtained from *Erianthus* Sp. other than *sara*.

The hybrids show more resemblance to sugar cane than *Erianthus* in their tall habit and the shape of the arrows. They resemble *Erianthus* in their stiff, very erect leaves, and in the slight development of the nodal triangles. Since the sugar cane parent was heterozygous, segregation in many characters, such as colour, thickness, length, etc., was exhibited by the F<sub>1</sub> hybrids, but in respect of the specific characters, the behaviour of the hybrids was uniform (Rümke, 1934).

Root tips of the *Erianthus* parents were found to possess 60 chromosomes (59 to 61). At meiosis 30 gemini occurred, and 95 per cent. of the pollen was fertile. The sugar cane parent had 80 somatic chromosomes, and a majority of the chromosomes formed gemini, though multivalent associations were observed. Secondary pairing was also noted. Up to 60 per cent. of good pollen formed.

Root tips of the hybrids examined exhibited on the average 67 chromosomes (from 60 to 70). Meiosis was irregular (e.g., 3 tetravalents, 23 bivalents and 8 univalents; 3 tetravalents, 24 bivalents and 6 univalents). Degeneration of pollen was noted, but in those hybrids in which anther dehiscence took place, there was 10 to 30 per cent. of good pollen.

Since the somatic number of the hybrids was always lower than the sum of the two parents, it would appear that gametes from E.K. 28 having less than the haploid number of chromosomes (owing to irregular separation of univalents) tend to give more fertile zygotes than gametes with the exact haploid number. Obviously no doubling of the chromosome complement of the sugar cane parent took place. (Rümke, 1934.)

As cane varieties are heterozygous, very little attention has been paid to the genetical constitution. Seedling hybrids always vary in a marked manner, but as the parental constitution was unknown and the main object of the cross was to obtain variability, genetic analysis was exceedingly difficult, if not impossible. Hybrids, however, have now been carried to the F<sub>2</sub> and subsequent generations,

and a number of selfed strains obtained and inter-crossed. As a consequence, Kutsunai (1926) and Venkatraman (1926) have started to analyze the inheritance of the fundamental morphological characters and also the all-important physiological characters upon which the economic value of the cane is largely based.

CLASSIFICATION.—The only satisfactory classification of sugar canes so far published is that of Jesweit (1916, 1925), based on the panicle characters.

Key to the species of *Saccharum* (after Jesweit).

- A. Main axis of inflorescence and cluster axes with long hairs. Glumes always 4. Lodicules either ciliate or not. If the spikelets of the same pair do not flower simultaneously, the pedicellate one always blooms first. Culms green, greyish-green, greenish-bronze, ivory or white.
- B. Lodicules ciliate, long subterranean runners present, growing wild . . . . . *S. spontaneum*.
- BB. Lodicules not ciliate. Subterranean runners short. Sugar-producing, cultivated plants.
- C. Leaves broad (to 50 mm.). Long cane species, nodes all fusiform, greenish-bronze (among others, Uba cane) . . . . . *S. sinense*, Roxb.  
amend Jesweit.
- CC. Leaves narrow, short inconspicuous cane species. Nodes usually cylindrical, greyish-green, white or ivory. Rather limited to British India (among others, Chunnee cane) . . . . . *S. Barberi*, Jesweit.
- AA. Main axis of inflorescence never having long hairs, often glabrate, rachis nodes glabrate or with very few hairs. Glumes generally 3, sometimes 4. Lodicules not ciliate. If the spikelets of the same pair bloom at different times, the sessile one always is the first. Culms differing in colour from pale or dark green to dark yellow, dark red, violet, often striped. Cultivated plant . . . . . *S. officinarum*.
- B. Fourth glume present. Vigorous plant with low sugar percentage. Types : among others, Fidji, Ardjoeno, Green Coerman (Corven Duitsch), New Guinea.
- BB. Fourth glume wanting. Plants with a general high percentage of sugar. Types : among others, Cheribon, Batjan, Borneo, Bandjermasia, Preanger.

A fifth species *S. robustum* has recently been discovered.

The more important of the varieties, especially the Noble canes of the East, have also been described by Jesweit and Becker. Many of the Indian canes have



been described by Barber (1915, 1918), who divided the Indian canes into five groups, Saretha, Sunnabile, Pansali, Nargori and Mundo. The first two of these, Saretha and Sunnabile, fall into Jesweitz's species, *S. Barberi*; the second three into his species, *S. sinense*. On the whole Bremer's analysis of the chromosome numbers supports Jesweitz's grouping.

The above classification, however, must be regarded as tentative. No genetic analysis of *Saccharum* can be said to exist, though a beginning has recently been made. The cytological analysis is by no means complete. Many descriptions of varieties have been published, but they, too, are incomplete, and essential differences await clearer and more concise expression. In all probability there still remain forms that are practically unknown. Certain minor differences (*e.g.*, the epidermal characters studied by Artschwager) have been insufficiently studied. Until our knowledge of these aspects has been extended and consolidated, no finality in classification can be obtained.

Sugar cane is generally believed to have had a dual origin. It has been argued that the thinner canes, such as the Indian canes, have a wild prototype in *S. spontaneum*; but the so-called Noble or thick canes are only known in cultivation and the wild prototype of these forms is (as yet) unknown. Jesweitz (1931) regards these canes (*S. officinarum*) as typical, and is of the opinion that the marked concentration of such types in N. Guinea indicates that area as the centre of diversity. There is no doubt a measure of truth in such conclusions, but in view of the incomplete knowledge we have, they must likewise be regarded as tentative.

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## CHAPTER X

### SORGHUMS

THE term "Sorghums" (Latin *surgo*—arise, so named because of the height of the plant) is here used comprehensively to include the many types of "grain sorghums", *Sorghum vulgare*, Pers., and the "grass sorghums", of which the most important is Sudan grass, *Sorghum sudanense*, Stapf.

#### 1. GRAIN SORGHUMS

(*Sorghum vulgare*, Pers. = *Andropogon sorghum* (L.) Brot.)

All the grain sorghums are annual.

**ROOTS.**—On germination, there is produced a primary seminal root which grows almost vertically downwards and produces throughout its length numerous lateral branches which, even in a seedling plant, may be 4 to 5 cm. long. No secondary seminals are produced. A few thin short roots, arising from near the base of the mesocotyl and therefore not true seminal roots, may occasionally be present. Sieglinger (1920) states that after the secondary roots begin to function, the primary seminal begins to decay. This may be the case, but the few observations of the author do not support the contention.

The later roots are all adventitious and develop in succession from the basal nodes situated just below to just above ground level. As regards number and extent in both a horizontal and vertical direction their growth is very similar to the roots of maize.

Weaver (1926) states that the superficial root system is very abundant, as plants with 6 to 8 leaves may have a lateral spread of 3 feet, the network extending to the surface and penetrating downwards perhaps not more than 1 to 6 feet. Later, the roots may have a working depth of 3 to 4 feet, and maximum depths of 4.5 to 6 feet may be attained.

They are, however, more fibrous than the roots of maize, and according to Miller (1916) develop more than twice as many laterals at any stage of their development. This would mean that the root system of a sorghum plant is about twice as efficient as the root system of a maize plant.

The profuse branching and wide distribution of the root system is one of the main reasons why the Sorghums are so markedly drought resistant. Other factors, however, are of importance. In the first place, the plant above ground grows slowly until the root system is well established. Secondly, the system has to supply a leaf area which is approximately half the leaf area of maize. Thirdly, the low transpiration rate must influence the water demand. Finally, the plant can remain dormant during a prolonged period of drought and thereafter re-continue its development.

This was formerly attributed to the depletion of the soil of water and available nutrients by the extensive root system. It has, however, now been demonstrated that the depression is mainly due to injurious decomposition products arising from the decay of the stubble and root (Sewell, 1923 ; Breaseale, 1924).

**STEMS.**—The stems are erect and solid, 3 to 15 feet high and slightly furrowed on alternate sides. The nodes are somewhat thickened ; the inter-nodes are short at the base, becoming longer above ; those of the middle region are nearly equal in length, but the terminal inter-node which ends in the head is the longest of all.

**Lateral branches.** The buds at ground level may develop as suckers, the number depending partly on the variety, partly on the environmental conditions. Up to 15 suckers may develop in certain varieties. These suckers are in the great majority of cases shorter than the main axis ; they may all develop " heads " which, however, mature later than that of the main axis.

Above ground level, there is a bud at each node, except the terminal node which is prolonged upwards as the peduncle and thereafter forms the rachis of the panicle. The development of these buds varies. After the main axis has headed, and often not until its seeds are half-ripe, the uppermost bud (the one at the node immediately below the terminal one) may elongate to form a true lateral branch, which generally develops a late maturing head. This is followed by a similar development of the lower buds from above downwards, so that under favourable conditions a considerable number of these laterals may form.

In general, the development of a large number of suckers, and especially the development of many laterals, is undesirable.

Rea and Karper (1932) have shown that Sorghums may be propagated by cuttings (see Fig. 137).

**LEAVES.**—The foliage leaves vary somewhat in the different varieties. The sheaths are long, in most cases exceeding the length of the inter-nodes, but considerable variation is found in different groups. Their margins are membranous and overlapping, markedly so in " Kaffirs ". The surface is practically glabrous with low ridges and the inner face is white and glistening. The ligule is short, membranous and fringed. In certain groups, as for instance Milo, the ligule may be situated at an angle of approximately  $45^{\circ}$ . The leaf blades are very similar to those of the maize plant. They are, however, more erect and the mid-rib is better developed. It would also appear that the leaf area of the Sorghums is less than that of maize. Taking the stages of growth in order (4, 6, 8 and 10 weeks), Miller (1916) found that the leaf area of maize was 1.7, 2.0, 2.2 and 2.3 times the leaf area of Dwarf Milo, and 1.6, 1.9, 1.5 and 1.5 times that of Blackhull Kaffir.

**PROPHYLLUM.**—The lateral buds are enclosed in a prophyllum, which later forms the first leaf of the lateral branch. It is a markedly compressed sheath, in outline flask-shaped, with the apex in the early stages drawn out into an acute point. The outer face is rounded ; the inner ridged ; the edges except at the base ciliate. Along the outer face, it is split from the apex to near the base, one margin markedly overlapping the other. If the bud develops into a lateral branch, the prophyllum elongates and splits along both sides, ultimately resembling two opposite leaves.

**INFLORESCENCE.**—The inflorescence, popularly known as the “head”, is a somewhat compact panicle, except in broom-corn and a few others, where it is loose and spreading.

The main axis is very varied in length. It may be reduced to a single node or may equal the length of the panicle with every gradation between. The expression, too, varies with the environmental condition. In all varieties and especially in the dense forms, it narrows towards the apex, its identity becoming lost in the terminal and at times the sub-terminal branches. The surface is either angular or variously furrowed, due according to Schumann (1895) to the pressure of the lateral branches on the axis during the early stages of development.



FIG. 137.

- A. Shoot and root growth of representative cuttings propagated in greenhouse bench.  
 1. Johnson grass ; 2. Tunis grass ; 3. Sudan grass ; 4. Honey Sorgho ; 5. Acme broom-corn ; 6. Standard Feterita ; 7. Standard Brown Koaliang ; 8. Mosshart yellow dent corn showing only root growth.
- B. Mature sumac sorgho plant grown from 2-node cutting, showing mother cutting attached. (After Rea and Karper.)

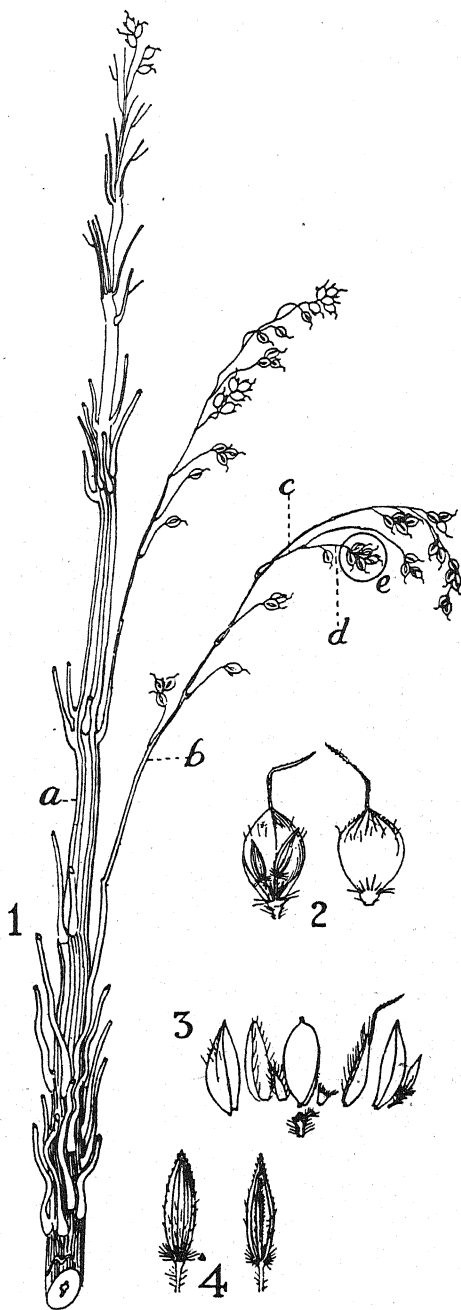


FIG. 138.

- 1, Axis of panicle, primary and secondary branches, racemes, and spikelets ; 2, fertile spikelet with sterile spikelets attached ; 3, fertile spikelet dissected and sterile spikelet, showing part of rachis segment, the glumes, sterile lemma, fertile lemma with awn, the palea, lodicules, and caryopsis of the fertile spikelet ; 4, sterile spikelet, showing pubescence of the pedicel and callus, the scabrous-hispid lateral nerves, and ciliate edges of the first glume. (After Cowgill.)

Pubescence varies. All forms are usually hairy at the nodes, often markedly so. The inter-nodes may be almost glabrous except for fine bristles or teeth on the ridges. Others may be finely hairy throughout; fringed on the ridges only; or scabridly hispid on the ridges. There is a tendency for the forms with longer inter-nodes to be more glabrous than those with shorter. The colour is generally the same tint as the peduncle, but in some it may approximate to the colour of the glumes.

At the nodes, lateral branches or rays develop. In lax forms, they appear to develop in whorls; in the denser forms, they simulate the appearance of a close spiral. Each lateral may re-branch, and branches of the third order may form. The ultimate branchlets bear one to several paired spikelets.

The length of the branches is very varied. They may be very long in broom-corn; intermediate, in effuse types; short to very short, in the compact types. The shape of the panicle, indeed, is ruled by the length of the main axis and especially the length of the laterals. As a consequence, the panicle may be markedly loose and spreading; more or less conical and spreading; conical and semi-compact; cylindrical and semi-compact; cylindrical and compact; elliptical and semi-compact; elliptical and compact; oval and semi-compact; and finally densely oval.

The lateral branches are usually somewhat angular, slightly devious to very rarely twisted. They are usually hairy at the base and at the axils, with the ridges finely hairy or bristly. The ultimate branches may be ciliate, scabrous or glabrous. They resemble in colour the main axis, but occasionally are tinted like the glumes.

In the spreading types of panicles and also, but to a less extent, in the compact types, pulvini occur in the axils of the branches. These pulvini tend to expand in mild weather, separating the laterals and so opening the panicle. Under dry conditions they contract and the panicles tend to close.

In certain groups (*e.g.*, Sorgho, Milo and Durra) the panicles become inverted. Ball (1910) has suggested the following terminology to describe the condition—erect, when not inclined more than  $45^\circ$  from the perpendicular; inclined, when the position varies from  $45^\circ$  to  $90^\circ$ ; declined, when  $90^\circ$  to  $135^\circ$ ; pendant, when  $135^\circ$  to  $180^\circ$ . The recurving has been attributed to the weight of the head, but there is little doubt that there exists an inherent tendency to the condition in many forms. Conner and Karper (1917) have studied the condition in Milo. They found that the main factor is the structure and development of the upper leaf sheath.

The peduncle in all types is slender, and in the early stages is so flexible that it requires the support of the sheath. If unsupported the head falls outwards by its own weight.

In Milo the sheath is rather thin and flexible and the attachment of the upper leaf to the sheath is oblique, averaging approximately  $45^\circ$ . One side of the sheath, and that the inner, is therefore longer than the other. As a consequence, the upper region is tightly infolded, and tends to remain so. As the head emerges, the pressure on the twisted sheath causes the leaf blade to describe almost a complete circle in a horizontal plane and, after emergence, the leaf swings back to its original position by describing another circle in the opposite direction. But in most cases, the inroll of the upper part of the sheath is so tight that, as the head pushes upwards,

the sheath tends to remain intact above, but splits below. The peduncle is accordingly unsupported on one side, and so tends to fall outward and downward.

Tall plants showed more inroll than dwarf plants, and therefore exhibited a greater tendency to produce pendant heads. Rapid growth was conducive to tallness; root-pruning and consequent limitation of pod increased the numbers of erect heads.

The spikelets usually occur in pairs on the terminal racemes, except towards the tip where they may occur in threes. When the spikelets are paired, one is sessile and perfect, the other pedicelled and staminate. When in threes, the one is sessile and perfect, the other two pedicelled and staminate; or at times, one staminate and the other perfect.

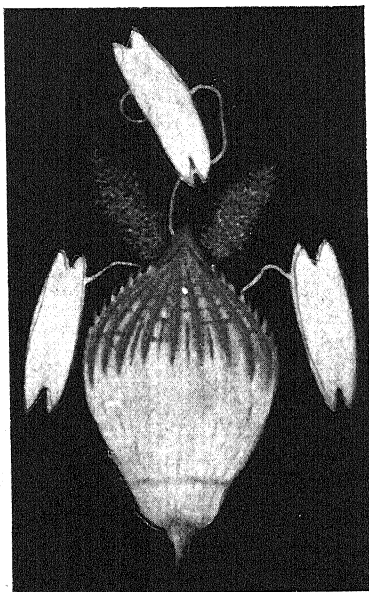


FIG. 139. Diagram of Sorghum spikelet at anthesis. (After Ayyangar *et al.*)

**FERTILE SPIKELET.**—The fertile spikelets are relatively large and the length in any one variety is fairly constant. The shape may be ovate, oval, elliptical or obovate, but it tends to change throughout the period of development. Each fertile spikelet has 2 glumes of about equal length. Both glumes are nerved, the number of the nerves varying from 6 to 18. The nerves of the outer glume are more conspicuous than those of the inner. In many cases, two of these nerves on the outer glume, one on each side, are prominent and keel-like; on the inner glume, there is but one prominent nerve, rendering it more or less centrally keeled. They may be gibbous at the base or more or less flat. The outer partially enwraps the inner which is narrower and more pointed at the apex. In texture they are leathery to chartaceous, with somewhat thickened base and membranous margins; they are hairy, but the pubescence is very varied. The colour varies from cream to differing shades of red and brown to black. At maturity, they may be from half to two-thirds the length of the seed, at times equalling the seed length.



Within the glumes 2 florets are found, the lower sterile, the upper perfect. Of the lower floret only the lemma is present, a broad, usually pubescent, membranous and somewhat truncate bract which partially enfolds the perfect floret. The second and perfect floret has a narrow membranous hairy lemma which is two-cleft at the apex. In the cleft an awn arises—short in some varieties, long and strongly protruding in others. When fully developed, the awn is twisted and geniculate in the middle. The palea, if present, is small and thin. The lodicules, two in number, are short and broad, truncate and fleshy, with long hairs at the margins. There are 3 stamens. The ovary has 2 long styles each ending in a short bushy stigma.

Triple-seeded spikelets were reported by Cron (1916) and similar multiple-seeded forms noted by Karper (1931).

**PEDICELLED SPIKELET.**—This spikelet is narrower and more pointed than the sessile one. It is borne on a short pedicel, which is angular and usually ciliate on the margins. Generally it becomes fragile and disarticulates by fracture. In some cases, however, it remains tough and tenacious, retaining the spikelet at maturity. Two leathery glumes enclose the 2 florets. The lower floret is represented by the lemma only. The upper floret may be staminate with a short, distinctly awned lemma, no palea, 2 lodicules and 3 stamens.

**ABNORMAL SPIKELETS.**—The normal fertile spikelet has one aborted and one functional floret, and therefore sets only 1 grain. Karper (1931), however, has found single spikelets which contained: 1, twin grains; 2, connate grains; 3, semi-connate grains and 4, triplets (*i.e.*, 3 separate grains).

When a single grain is present (the normal condition), the embryo is situated on the ventral side next the inner glumes. When 2 grains are present, they are "back to back", the extra grain having the embryo on the dorsal side next the outer glume.

Connate seeds develop as twins within the same pericarp, and have two fully-developed embryos. Semi-connate seeds vary between these two extremes. Coalescence ranges from a union at the base only to a condition approximating to the true connate condition. When triplets are present, the grains are free from one another.

Karper considers that "the most probable explanation of these abnormal spikelets seems to be that, under certain conditions, both flowers are functional and that furthermore, the primordia of a third flower is at least sometimes, if not always, present in the spikelet and that this flower sometimes becomes functional." In support of this contention, it should be noted that Long (1930) has demonstrated the presence of meristematic tissue of a first flower and a rudimentary bundle thereto in both Johnson grass and Sudan grass.

**ANTHESIS AND POLLINATION.**—The first flowers to open are those near the tip of the main axis. Thereafter, anthesis proceeds downwards. Of a pair of spikelets, the sessile generally opens before the pedicelled. Most of the flowers open in the early morning. Thus Graham (1916) at Nagpur, India, found that the maximum period was between midnight and 4 a.m.; the stigmas usually appear first and as the glumes fall apart, they separate and the stamens appear on the rapidly lengthening filaments. The whole process is so rapid that it may be seen with a lens and is complete within some minutes of its inception.

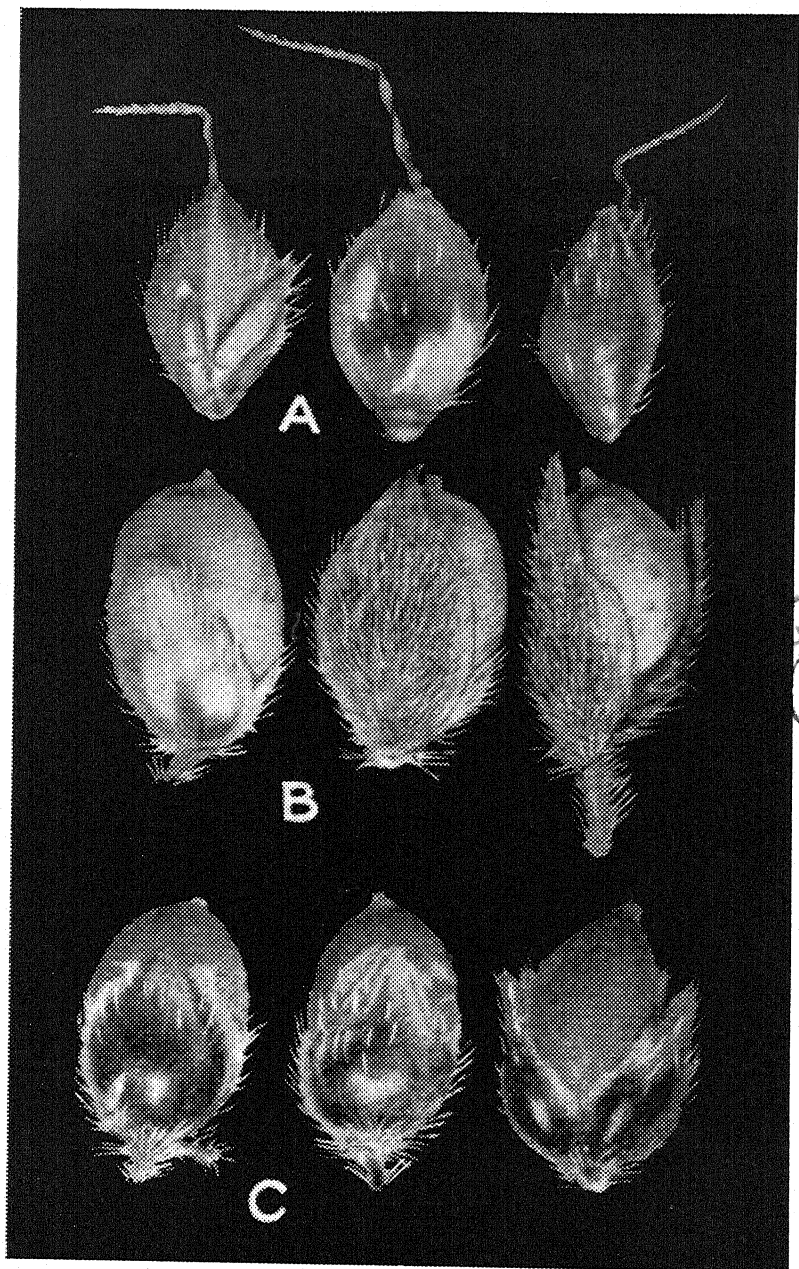


FIG. 140. Fertile Spikelets of Three Varieties of Sorgho. X 8.

A. Honey (Sugar Plant No. 0241466); elliptic and obovate-elliptic spikelets; pubescence semideciduous; awn somewhat loosely twisted; caryopsis not extending as far as the glumes. B. Planter (Sugar Plant No. 01816); ovate-elliptic spikelets; pubescence more persistent except where the glumes are considerably indurate; caryopsis extending as far as the apices of the glumes. C. Silvertop (Sugar Plant No. 021618-23); elliptic-ovate and ovate spikelets; pubescence semideciduous except on the callus, where the hairs are somewhat longer and more persistent; caryopsis extending beyond the apices of the glumes. (After Coville)

Ayyangar and Rao (1931) at Coimbatore, India, studied six varieties and found that anthesis in all commenced at midnight and continued usually until 8 a.m., sometimes prolonged to 10 a.m. Stephens and Quinby (1934) in Texas, U.S.A., obtained the following average peak figures—for Blackhull Kaffir, between 11 p.m. and 1 a.m.; for Spur Feterita and for Chinese Amber sorgo, between 1 and 2 a.m.; for Standard Yellow milo, between 5 and 6 a.m. They found further, that in all varieties the hour of maximum blooming fluctuated from night to night and that there was no period in which some flowers were not open.

Stephens and Quinby also found that the total duration of flowering on a panicle averaged 6 to 9 days, though late in the season some varieties bloomed for 15 days.

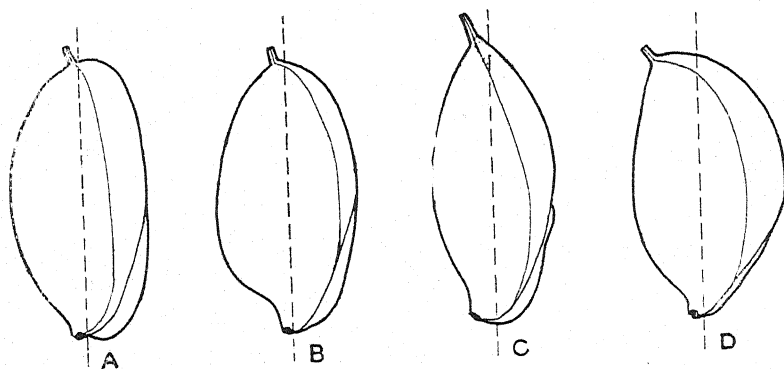


FIG. 141. Caryopses of Four Varieties of Sorgho.

- A. Minnesota Amber.
- B. Folger.
- C. Orange.
- D. Red X.

The differences in conformation are in part due to differences in curving. (After Cowgill.)

The anthers usually begin to dehisce as they become pendant by two narrow slits at their apices. At this stage, anthers and stigmas are practically in contact, and as the stigmas are already receptive self-pollination occurs. Pollination between flowers of the same panicle is also very frequent, and true cross-pollination readily occurs. (Graham, 1916; Fruwirth, 1923; Ayyangar and Rao, 1931.)

Ball (1910) found the amount of natural crossing between adjacent rows to rise as high as 50 per cent. Most of the other investigators obtained lower figures—Graham (1916) 0.6 to 20 per cent.; Karper and Conner (1919) an average of 6 per cent.; Kottur and Kulkarni (1922), 0 to 11.9 per cent.; Patel, 25 per cent. between rows 3 feet apart; Kottur and Chavan, 0 to 12 per cent. Patel and Patel (1928), however, again found up to 50 per cent., but climatic conditions had a marked effect.

According to Stephens and Quinby (l.c.) individual flowers of Spur Feterita averaged 7 minutes to become completely open, 20 minutes to begin closing and 2 hours and 7 minutes to become completely closed. Pollen production is very high; Stephens and Quinby counted almost 5,000 grains in each of 2 anthers

of Spur Feterita, approximately 15,000 per flower. In this variety, the average number of hermaphroditic flowers on 4 panicles was found by them to be 1,600. Such a panicle would, therefore, produce an average of over 24,000,000 pollen grains.

The pollen germinates immediately and retains its vitality for only a short period. The stigmas, however, are receptive to pollen some time before the flowers open, and may remain receptive for a considerable period after flower opening. Thus, Stephens and Quinby (l.c.) obtained seed from anthers pollinated

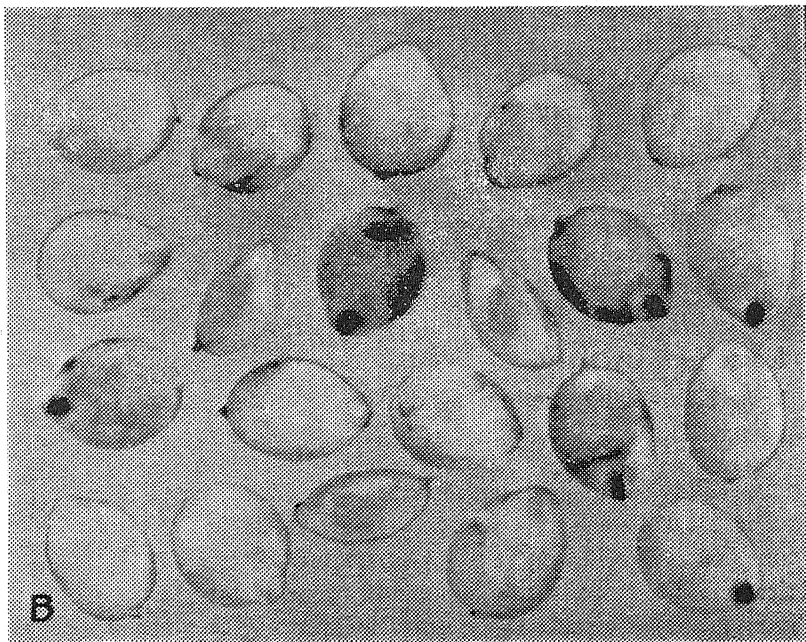


FIG. 142. Caryopses of Red Amber Varieties of Sorgho. X 5.

Caryopses of Red Amber (Sugar Plant No. 01826); elliptic and obovate-elliptic, rounded at the summit; style bases usually turned ventrally. (After Cowgill.)

8 days after blooming during midsummer and during the end of the season (October), 16 days thereafter.

Fertilization takes place from 6 to 12 hours after pollination. (Stephens and Quinby, l.c.)

**CARYOPSISIS.**—The mature grains vary in shape and colour. They may be white, yellow, red, brown or black with intermediate shades. The Kaffirs, Kowliangs and Shallus tend to be globular; the sweet sorghums pear-shaped; the Durras flattened. One surface is always more or less flattened, and carries the embryo at its base. On the opposite side, an oval brown area at the base marks the point of attachment; and on the rounded apex, the remains of the style branches are usually obvious as two claw-like points.

Two faint lines extend upwards from the scar or hilum past the scutellum to the bases of the style remnants. Sometimes a third line can be detected between these two. They consist of strands of elongated cells associated with vascular bundles. In some varieties, also, the ventral surface is transversely wrinkled. The grain is more or less enclosed by the glumes in some varieties, in others it is free.

The grain coats present certain unusual features (Winton, 1902).

PERICARP.—a. *The epidermis* (Epicarp).—Elongated cells with thick waxy walls, and fairly distinct pores. The external cuticle is of uneven thickness.

b. *The outer parenchyma* (Hypoderm).—Two or three layers of cells resembling the epidermal layer but with somewhat thinner walls.

c. *Middle parenchyma* (Mesocarp).—Here the cells are thin-walled, and frequently contain numerous small, round or somewhat polygonal starch granules, which tend to disappear as the grain ripens. As this layer contains chlorophyll until nearly mature, the starch may be formed *in situ*. The thickness of this layer varies to a marked degree in different varieties.

d. *Cross cells*.—A single layer of long narrow cells at right angles to the former cell layers.

e. *Tube cells*.—The product of the inner epidermis of the ovary. They become isolated and are about  $5\ \mu$  wide, up to  $200\ \mu$  long.

TESTA. This layer is unusually thick, being at times  $50\ \mu$  wide. The outer and radial walls are thin but the inner walls are much swollen. The layer is also conspicuous for its yellow to brown colour.

Pericarp and testa constitute about 6 per cent. of the grain.

Winton (1902) also states that a nucellar layer may be present in certain types.

Swanson (1928) investigated the colour of the grain in relation to the structure of the coat. Pigment when present was found to occur in the epidermal and hypodermal cells of the pericarp (pericarp colour) and (or) in the "nucellar layer". This "nucellar layer" according to Swanson varied in development. In some varieties it was strongly developed; in others much reduced; in one variety it was represented by a trace; in eight varieties it was absent.

The following table from Swanson gives the thickness of the coats, the distribution of the pigment and the possible factorial constitution of the varieties studied by him.

That the layer referred to by Swanson (1928) as the "nucellar layer" is in reality derived from the nucellus, is open to question. The only massive layer beneath the pericarp in sorghums is the testa (inner integument). According to the writer's observations, it also varies in thickness. A massive integument is also found in Johnson grass and a less massive one in Sudan grass. (Harrington and Crocker, 1923.) All the evidence seems to indicate that Swanson's nucellar layer is the "testa" (inner integument).

TABLE XXXII.

THICKNESS OF THE VARIOUS SEED-COAT STRUCTURES, PIGMENT LOCATION, SUPERFICIAL SEED COLOUR, AND POSSIBLE COLOUR FACTORIAL CONSTITUTION OF REPRESENTATIVE SORGHUM VARIETIES.

(Data from Swanson.)

Sorghum variety.	Thickness in microns of				Location of pigment.	Possible factors for colour inheritance.	Notes.
	Pericarp including nucellar layer if present.	Nu- cellar layer only.	Pericarp.				
			Meso- carp only.	Epider- mis, hy- poderm, and cuticle.			
Feterita ..	140	55	70	15	Nucellar	<i>Bsr</i>	Chalky - white pericarp
Dwarf hegari ..	140	56	77	7	do.	<i>Bsr</i>	Colourless pericarp with small reddish specks.
Manchu brown koaliang ..	140	35	70	35	{Nucellar} {pericarp}	<i>BsR</i>	Walnut - brown pericarp
Red Amber ..	110	60	10	40	do.	<i>BSR</i>	Reddish-brown pericarp
Broom-corn ..	95	45	10	40	do.	<i>BSR</i>	Amber to wal- nut - brown pericarp
Kansas Orange	85	25	25	35	do.	<i>BSR</i>	Walnut - brown pericarp
Darso .. ..	80	30	28	22	do.	<i>BSR</i>	do.
Schrock ..	125	45	50	30	do.	<i>BSR</i>	do.
Sudan grass ..	30	15	Trace	15	do.	<i>BSR</i>	Chocolate- brown pericarp.
Pink Kaffir ..	78	3	50	25	do.	<i>BSr</i>	Colourless pericarp with pinkish specks or blotches
Dawn Kaffir (Dwarf Black-hull) ..	70	Absent	40	30	Absent	<i>bSr</i>	Colourless pericarp with small reddish-brown specks or blotches
Sunrise Kaffir	80	Absent	45	35	do.	<i>bSr</i>	do.
Reed Kaffir ..	75	Absent	45	30	do.	<i>bSr</i>	do.
Red Kaffir ..	45	Absent	20	25	Pericarp	<i>bSR</i>	Eng. red pericarp
Freed Sorgo ..	65	Absent	30	35	Absent	<i>bSr</i>	Colourless pericarp
Shallu ..	50	Absent	10	40	do.	<i>bSr</i>	do.
Yellow milo ..	65	Absent	45	20	Pericarp	<i>bSR</i>	Ochraceous - salmon yellow pericarp
White milo ..	75	Absent	40	35	Absent	<i>bSr</i>	Colourless pericarp

**ENDOSPERM.**—The aleurone is a single layer, its cells very variable in size and shape.

The endosperm proper is divisible into two parts—an outer shell of horny endosperm which does not reach the embryo, and a central core of starchy endosperm. The polygonal starch grains, each with a distinct hilum and radiating fissures, are fewer and smaller to the exterior, becoming larger and more numerous to the interior. They are surrounded by small protein granules, which may fill the outer cell layers to the exclusion of the starch. Kempton (1921) reported the discovery of Sorghum from China and the Philippines with waxy endosperm.

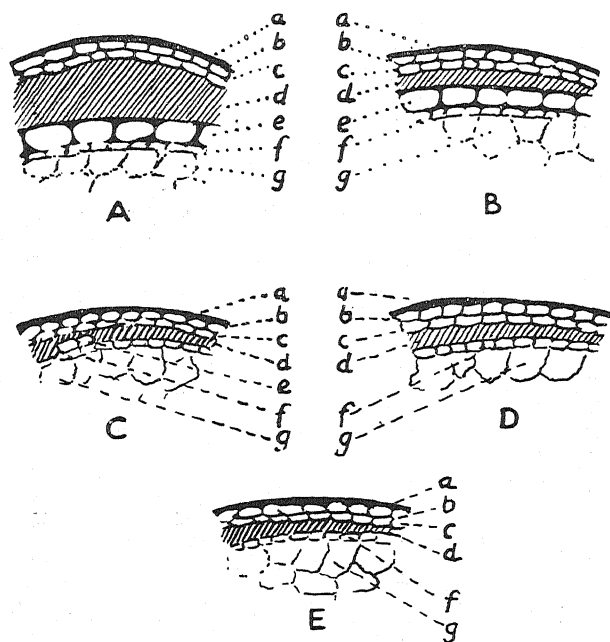


FIG. 143.

Diagrammatic sections of the seed coats of five sorghum varieties: *a*, cuticle; *b*, epidermis; *c*, hypoderm; *d*, mesocarp; *e*, nucellar layer; *f*, aleurone; *g*, endosperm.

- A. Feterita; colourless epidermis and hypoderm; highly developed mesocarp and nucellar layer.
- B. Red Amber; coloured epidermis and hypoderm; thin mesocarp, nucellar layer.
- C. Black Hull Kaffir; colourless epidermis and hypoderm; thin mesocarp and nucellar layer absent except for slight remnants.
- D. Yellow milo; coloured epidermis and hypoderm; thin mesocarp, nucellar layer absent.
- E. Freed sorgo and White milo; colourless epidermis and hypoderm; thin mesocarp, nucellar layer absent. (After Swanson.)

**Embryo.** The embryo of Sorghum very closely resembles that of maize. There are, however, no preformed secondary seminal roots.

The composition of the Sorghums and the relative proportions of the various parts may be gathered from the following table (Bidwell (1918), "A Physical and Chemical Study of the Kaffir Kernel").

TABLE XXXIII.  
COMPOSITION OF SORGHUM PARTS.  
(Data from Bidwell.)

Sample.	Per cent. of whole grain.	Ash. per cent.	Ether extract. per cent.	Crude protein (N $\times$ 6.25). per cent.	Crude fibre. per cent.	Nitrogen free extract. per cent.	Pento- sans. per cent.	Starch. per cent.
1. Whole grain ..	100.0	1.8	4.1	12.7	1.8	79.6	3.3	61.9
2. Pure endosperm ..	83.9	.3	.7	12.7	.8	85.5	1.9	69.3
3. Pure germ ..	10.0	13.2	31.5	19.3	3.8	32.2	6.1	—
4. Pure bran ..	6.1	2.0	6.8	4.8	16.2	70.2	18.4	—
5. Starchy endosperm ..	35.0	.3	.8	10.1	.8	86.5	1.9	70.4
6. Horny endosperm ..	48.9	.3	.7	13.7	.7	83.8	1.6	68.8



CLASSIFICATION.—Linnaeus (1753) described the species of *Sorghum* under the genus *Holcus*. These were *Holcus sorghum*, *Holcus saccharatus* and *Holcus halepensis*. The third species is the wild Johnson grass; the first two were cultivated forms from India. Later (1771) he restricted his species *H. sorghum*, and added a fourth, *Holcus bicolor*. In 1775, Forskal described two more species from Egypt, viz., *H. dochna* and *H. durra*. Arduino (1786) gave detailed descriptions of six species; three were new; the others were those described by Linnaeus. He was the first to grow and study the forms he described in the field. In 1804, Brotero transferred *H. sorghum* and *H. halepensis* to the genus *Andropogon*, and a year later, Persoon revived the generic name *Sorghum*, first proposed by Micheli.

The first description of the forms imported into America were published by Olcott in 1857. Later, Pech (1866) and Collier (1884) attempted a natural classification. Körnicke (1885) presented a classification of all the known forms under the one species *Andropogon sorghum* (L.) Brot. He divided the species into two sections—Effusus with five varieties, and Contractus with seven varieties; each section was again subdivided into two groups, the first on the length of the rachis, the second on the nature of the panicle, whether erect or recurved. His varieties were finally differentiated mainly on the panicle form and the colour of the glumes and the caryopsis.

Hackel (1890) described 36 cultivated types as varieties of *A. sorghum* sub-species *sativus* (= *A. sorghum* of Körnicke and *Sorghum vulgare* of Persoon). He utilized botanical characters throughout, many of which tend to vary in the field.

The development of European colonies in tropical Africa led to the study of the Egyptian, East, West and Central African forms. In 1895, Schumann published a classification of types from German East Africa; Busse and Pilger (1902), those of the same region with Togo; Dumas (1905) the forms of the Niger and Senegal. In 1917, Stapf issued his classification of the African forms in Prain's *Flora of Tropical Africa*. It is based wholly on detailed botanical characters. All the varieties are treated as belonging to the species *Sorghum vulgare*. This classification (though based on herbarium material) was the most comprehensive published until the publication of Snowden's (1935, 1936).

Snowden's classification—first issued in synopsis in 1935—has since been published in detail under the title *The cultivated races of Sorghum* (1936). He divides the genus into two sections, Eu-Sorghum and Para-Sorghum, the former again divided into two sub-sections.

*Sorghum vulgare* is drastically divided into five sections with a total of twenty-seven species (or sub-species). Unfortunately, this classification was received too late for critical consideration.

The very numerous forms of Sorghums in India have not yet been studied in detail. There are scattered references throughout the early literature. The first general account published was that of Hooker (*Flora of British India*). Benson and Subba Rao (1906) gave the first classification with reference to the agronomic characters. Since then, Graham (1916), Kottur (1919), Patel and Patel (1928) have made important contributions.

According to Ball (1910) the Chinese forms belong mainly to one type, the "Kowliangs". No local studies of the forms, however, have been made.

Adequate studies of the Egyptian and Sudanese forms have not yet been published. Stapf's references to the S. African forms in *Flora Capensis* are inadequate. Ivanov (1930), however, has recently issued an account of the Sorghums of N.E. Africa and S.W. Arabia. Beyers (1930) has studied the S. African Broom-corns and du Preez (1931) attempted a provisional classification of the S. African Kaffir-corns.

Breakwell (1918) published an account of the varieties introduced into Australia.

The most comprehensive studies from the agronomic standpoint have been those published in recent years in the United States. The classifications, however, are based on the local cultivated introductions, and are somewhat difficult to correlate with the partial classifications that have been issued on indigenous varieties elsewhere.

Practically the whole of this work has been done by Ball and his collaborators. His first classification was published in 1917, and has from time to time been revised. The keys issued to date now include most if not all of the cultivated forms of the U.S.A. The Texas forms have recently been described by Karper, Quinby, *et al.* (1932).

## SYNOPSIS OF THE GROUPS

- |  |                          |
|--|--------------------------|
| A. Panicles definitely umbelliform   | I. BROOM-CORNS.          |
| AA. Panicles not umbelliform, though varying<br>from effuse to contracted. |                          |
| B. Pith markedly juicy   | II. SACCHARINE SORGHUMS. |
| BB. Pith slightly juicy to dry   | III. GRAIN SORGHUMS.     |

### I: THE BROOM-CORNS.

The origin of the Broom-corns is obscure, but the evidence available indicates that it arose in Italy over 250 years ago. Casper Bauhin (1658) states that the slender heads were made into brooms by the Italians, and Ray (1688) makes a similar reference. The type must have been selected from a markedly effuse panicked form but exactly when and from what stock cannot be ascertained, though it should be remembered that the Sorghum plant (according to Pliny) was introduced into Italy from India about A.D. 60.

The Broom-corns may be tall or dwarf, varying from 3 to 13 feet in height. The stems are solid and pithy, with the inter-nodes longer than the sheaths. The exertion of the peduncles, however, varies. In dwarf types it tends to be somewhat poor. The panicle is erect, at times pendant. In most cases it is not the peduncle that is recurved, but the axis and its branches 1 to 3 inches above the base of the panicle.

In all cases, the panicle is umbelliform, the main axis not exceeding one-fifth of the length of the head, with the laterals crowded, much elongated and of approximately equal length. Both axis and laterals tend to be tomentose, especially at the axils. Each lateral is lenticular in outline, distinctly furrowed, with the inner face

becoming flattened above. The branches of the second and third order are slender and appressed. All the laterals tend to be devious at the base ; above they may be more or less straight to markedly wrinkled. Towards the apex, the branches are all twisted, and tend to interlace. The spikelets are borne singly or in groups of two to five and are in outline elliptic-oval to obovate. At the base they are often markedly ciliate, the cilia passing upwards on to the glumes, which are tan to reddish in colour. The lemmas are awned to semi-awned. The seeds are reddish and generally included.

Sieglinger (1928) has given the following key to the American groups.

- A. Plants tall (usually 7 to 13 feet).
- B. Peduncle usually 8 inches long or longer, firmly attached at the base ; panicle fully exerted from sheath . . . . . *Standard.*
- AA. Plants short (usually less than 6 feet and rarely 8 feet in height).
- B. Peduncle usually less than 8 inches long, weakly attached at the base ; panicle not fully exerted from the sheath.
- C. Plants usually 5 to 6 feet in height ; fibres coarse usually 20 to 24 inches long . . . . . *European Dwarf.*
- CC. Plants usually 4 to 5 feet in height ; fibres usually 16 to 22 inches long . . . . . *Western Dwarf.*
- CCC. Plants usually 3 to 4 feet in height ; fibres fine, usually 12 to 18 inches long. . . . . *Whisk Dwarf.*

In South Africa the locally grown dwarf types belong almost entirely to the European Group. There also appear to be types which do not correspond precisely with the above groups. (Beyers, 1930.)

## II. THE SACCHARINE SORGHUMS.

The Saccharine Sorghums or briefly the "Sorgos" are characterized by having a sweet juicy pith, in contrast to the non-saccharine or grain sorghums.

The plants are somewhat tall, varying from 5 to 10 feet in height. They produce suckers but moderately ; branches from the upper buds may form, but at times only towards maturity of the main axes.

The sheaths are typically long, completely covering the inter-nodes, but varieties with the inter-nodes not covered are known. The peduncles are straight or recurved, but the number of recurved forms and the degree of recurvature when present are variable. There are fairly well-marked differences in the length of the peduncle and the length of the terminal leaf sheath and, as a consequence, in the degree of exertion. Both recurvature and exertion, however, are influenced by soil and season.

The panicles vary from the somewhat spreading effuse type to the compact type. This is mainly due to differences in the length of the axis, the length of the branches and in the degree of rigidity developed in the latter. The pubescence varies from a pilose to a more or less scabrose condition.

The spikelets vary from 0.1 to 0.25 inches and are typically ovate, elliptic or obovate in shape. The glumes are somewhat variable in shape, texture, pubescence and degree of thickening, etc. Their colour ranges from pale yellow to deep black. Awns, though variable, are either present or absent.

The caryopses differ in shape, but in any one variety the type is fairly constant. In colour, they are usually lighter than the glumes, ranging from white through tints of yellow, brown, reddish-brown to chocolate-brown. They may be moderately exserted to almost completely enclosed by the glumes.

The sterile spikelets are somewhat deciduous, generally fracturing fairly readily from the pedicels which tend to turn brittle as they mature. In some varieties the sterile spikelet is very prominent.

Ball (1907 up to 1922) has issued a classification of a number of the varieties grown in America, and Cowgill (1926) has studied the panicle characters in particular, and added a synopsis of the varieties with detailed descriptions of approximately twenty.

### III. THE NON-SACCHARINE OR GRAIN SORGHUMS.

Ball's analysis of this section (modified) is as follows :

- I. Spikelets oval or narrowly obovate, 2 to 4 mm. wide ; seeds mid-sized to small, ovoid, scarcely flattened :
  - I. *Kaffir, Koaliang, Shallu Group.*
- II. Spikelets broadly ovate, 4.5 to 6 mm. wide ; seeds large, lenticular, flattened ; panicle oval-ovate, short-branched, compact :
  - II. *Durra-Milo Group.*

#### I. KAFFIR, KOALIANG, SHALLU GROUP.

This group is differentiated as follows :

- |   |                      |
|---|----------------------|
| A. Stems stout, somewhat juicy ; inter-nodes short ; leaves 12 to 15, broad, usually dark green . . . . . | <i>A. Kaffirs.</i>   |
| AA. Stems slender, dry ; inter-nodes longer ; leaves 7 to 10, narrower and lighter green.                 |                      |
| B. Panicle compressed ; glumes lightly appressed to the brown or white seeds . . . . .                    | <i>B. Koaliangs.</i> |
| BB. Panicle conical, loose ; glumes spreading, exposing yellowish-white seeds . . . . .                   | <i>C. Shallus.</i>   |

A. *Kaffir-Corns or Kaffirs.*—The plants are erect to spreading in habit, and vary from 4.5 to 9 feet in height.

The stems are stout, tapering towards the apex, dry and pithy or juicy, but less sweet than in the Sorgos. The inter-nodes are short to medium in length, entirely covered by the leaf sheaths, especially so in the dwarf types. Tillering and branching are very varied. The leaves are 9 to 15 in number, dark green in colour, long and broad, turning to semi-erect to more or less erect in habit.

The peduncles vary in length but the exsertion is usually fairly good and on the average better than is the case in the other grain sorghums. Recurvature is not known.

The panicles are usually fairly compact and oval, elliptical, cylindrical to conical in shape, but mostly elliptical to cylindrical. The rachis in most cases is distinct, and pubescent to semi-pubescent. The fertile spikelets are 3 to 7 mm. in length, oval to obovate in shape. The glumes are somewhat variable in shape, thin to thick, soft and pliable to hard and brittle. In colour they vary from yellowish-white to black, and light- and dark-coloured glumes may occur on a single panicle. The lemmas are awnless.

The seeds are usually medium in size, ovoid and scarcely flattened; white, pink, red to purple in colour; never enclosed at maturity by the glumes.

Du Preez (1931) has prepared a tentative key to the S. African types.

B. *Koaliangs*.—The term *Koaliang* was applied by Ball to forms imported from China, and is in all probability far too comprehensive. Apparently no local studies of the types have been made.

The habit is erect, the average height being 7 feet.

The stems are somewhat slender, with but slight taper, and are dry and pithy. Tillering and branching is low. The inter-nodes are of moderate length, with the exsertion of the head poor.

The leaves are 7 to 10 in number, evenly distributed, somewhat short and broad, dark green and turning in habit.

The panicles are long, more or less open in form, compressed, cylindrical and erect. The rachis is glabrous and distinct.

The fertile spikelets are 5 to 7 mm. long, and oval in shape; the glumes are ovate in shape, semi-pubescent, dark red to brown in colour, and somewhat thin, soft and pliable. The lemmas are distinctly awned. The grains are fairly large and elliptical; white, red to brown in colour; with the appressed glumes at maturity covering about three-quarters of their length.

C. *Shallus*.—The plants are somewhat spreading in habit with thin slender stems, dry, pithy and with little taper, and may reach a height of 5 to 8 feet. Tillering is often marked, but there is little branching. The leaves are 7 to 10 in number, usually light green, long and turning in habit; the sheaths generally completely cover the inter-nodes.

The panicles are erect, conical, very open and ultimately somewhat one-sided. The rachis nearly equals the length of the head and is more or less glabrous. The spikelets are small, ovate to elliptical in outline; the glumes are yellowish-white in colour, ovate to elliptic in shape, in texture somewhat hard and brittle. At first they are closely appressed, but later open widely. The lemmas are awnless.

The grains are small, yellowish-white in colour, hard and vitreous in texture.

The *Shallus* are poor grain producers, and economically of minor importance.

## II. DURRA-MILO GROUP.

Carleton Ball has subdivided this group in the following manner.

A. Glumes greenish-white, densely pubescent, not transversely wrinkled; seeds much flattened.

A. *Durra*.

AA. Glumes dark brown to black, thinly pubescent to glabrate, transversely wrinkled; seeds less flattened.

B. Panicles narrowly oval, always erect ; lemmas not awned ; seeds chalky or bluish-white .

B. *Feterita*.

BB. Panicles broadly oval or ovate, inclined to pendant ; lemmas awned ; seeds white or brown . . . . .

C. *Milo*.

A. *Durras*.—The plants are semi-erect in habit, with stems 4 to 6 feet in height, of medium thickness, and tapering but slightly, dry and pithy in texture. Tillering and branching is much reduced. The leaves are few in number, dark green, somewhat short but broad and twining in habit. The sheaths are short and do not cover the inter-nodes. Exsertion is usually very poor.

The heads are short and strongly compact, oval to oval-oblong, erect to frequently pendant. The rachises are usually long and markedly pubescent.

The spikelets are 4 to 6 mm. long, ovate to obovate in outline, with appressed, strongly pubescent, greenish-white glumes which are slightly thickened, somewhat hard, brittle and without transverse wrinkling. The lemmas are awned or awnless. The grains are fairly large, white or brown in colour, firmly enclosed by the glumes. In shape they are orbicular and rhomboidal and distinctly flattened.

There are at least two types of Durra, the white seeded awned forms, and the brown seeded and awnless forms.

B. *Feteritas*.—The Feterita types are Egyptian in origin, and are somewhat intermediate in their characters between Durras and Milos.

The plants are erect and fairly vigorous in habit. The stems are slender with little taper, dry and pithy, ranging from 5 to 6 feet in height. Tillering and branching are generally marked, with the heads on the branches standing above the heads on the main culms.

The leaves are 8 to 9 in number, evenly distributed, of medium length, somewhat narrow, light green in colour, and twining in habit. The sheaths do not cover the inter-nodes. Exsertion is generally good.

The heads are erect and short, somewhat compact, oval to ovate in shape and pointed towards the apex. The rachis is distinct with short inter-nodes and distinct pubescence.

The fertile spikelets are 5 to 7 mm. long, orbicular to obovate in shape. The glumes are appressed, covering half to two-thirds of the seed, ovate to rhomboidal in shape, pubescent, dark brown in colour, without transverse wrinkling and thick, hard and brittle in texture. The lemmas are awnless.

The grain is fairly large, chalky to bluish-white in colour and soft in texture.

C. *Milos*.—The plants are semi-erect to spreading in habit. The stems are slender to medium in thickness, tapering but slightly, dry and pithy, from 3.5 to 6 feet high. They tiller strongly with fairly heavy branching.

The leaves are 8 to 10 in number, fairly evenly distributed, somewhat short and narrow, dark green in colour and twining in habit. The leaf sheaths are shorter than the inter-nodes. Exsertion is generally poor.

The heads are erect to pendant, short, somewhat compact, oval to shortly ovate in outline. The rachis is distinct, with short inter-nodes and semi-pubescence.

The fertile spikelets are 5 to 6 mm. long, orbicular to shortly obovate, with the glumes appressed and covering half to two-thirds of the seed. In outline, the

glumes are rhomboidal, yellowish-white to brown in colour, semi-pubescent, with very distinct transverse wrinkling, of medium thickness, fairly hard and brittle. The lemmas are awned.

The grains are orbicular to shortly obovate, scarcely flattened, white, yellow or brown in colour, of medium hardness, and (proportionately) a large embryo.

**ORIGIN OF GRAIN SORGHUMS.**—In the past, it was at first generally conceded that the Sorghums were derived from the wild species *Sorghum halepense* (*Andropogon halepensis* (L.) Brot.), which is common in all tropical and sub-tropical parts of the Old World. This species is a variable one, and its numerous forms are said to parallel the more important cultivated types. "This is especially noticeable in comparing the forms assumed by the wild and cultivated species in Africa and to a less extent in India also. The abundant variation of the wild species, the great number of different cultivated forms, and with few exceptions, their evident dissimilarity in the two regions argue for independent origin of the cultivated forms on the two continents."

It should be noted, however, that *Sorghum halepense* is perennial and that all varieties possess well-developed root stocks. So far as the African continent is concerned, *S. halepense* is found as a wild species in the Northern regions only, and does not extend into the more tropical districts. In these districts the wild species are annual without root stocks and belong to Piper's so-called grass sorghums. The more important species are *Sorghum sudanense* (Sudan Grass), which is cultivated in Egypt and occurs more or less wild in the Sudan; *Sorghum virgatum* (*Tunis Grass*), indigenous to the Sudan; *Sorghum effusus* from the West African coast; *Sorghum verticillatus*, indigenous from South-East Africa to the Cape. It should also be noted that *S. halepense* has 20/40 chromosomes (Longley, 1932; Huskins and Smith, 1932) whilst all the grain sorghums have 10/20 chromosomes. Also, Huskins and Smith suggest that *S. halepense* may be an auto-tetraploid of one of the annual forms. These facts would appear to indicate that the Grass Sorghums are the parent forms of the Grain Sorghums.

The originals of the known cultivated races must accordingly be looked for in Africa and India. This is no easy matter as even a superficial study of the indigenous types cultivated in the two continents reveals the presence of a very large number of types, mostly undescribed.

S. Africa (Natal, Zululand and the Northern Transvaal) is the home of the sweet sorghums (Sorgos) and the so-called "Kaffirs". Other types undoubtedly exist, but some may have been introduced. Very little is known of the Sorghums of Equatorial Africa. On the West coast, several types exist, one series showing a peculiar lateral rotation of the seed relative to the glumes at maturity (Hackel's *v. ovulifer*), the other series being closely related to the Shallus. On the East coast, there exist representatives of the "Kaffirs", forms approaching the Sorgos and others which consist of entirely new groups of which little or nothing is known.

In Egypt all Sorghums are termed durra; three varieties are widely cultivated, Beda, Safra and Alnuar, white, yellow and brown seeded respectively. Of these Safra is probably the original of the cultivated milos. Along the Mediterranean basin, Morocco, Algeria, Tunis, etc., the leading variety is a white durra, which may or may not be indigenous. South-West Asia possesses certain varieties which

of these is akin to the cultivated durras; of the remainder one minor group constitutes the so-called rabi crop, which is sown not in spring but in autumn. It is mostly composed of a single group, the Shallus.

In China there exists a single indigenous group, the Kowliangs, which have probably been derived from introductions from India many centuries ago. Broom-corn was developed in Italy more than 250 years ago. Its parent, or parents, must have been a loose-panicled sorghum (or sorghums), of unknown variety.

**INHERITANCE AND HYBRIDIZATION.**—Until recently, comparatively little work has been done on the genetics of Sorghum.

Sieglinger (1932) found two factors operative for height in Broom-corn. In the commercial dwarf varieties, one of each of the factors was absent. Pithiness of stem was found by Hilson (1916) to be dominant, and a correlation was claimed by him to exist between a continuous white line along the length of the mid-rib and pithiness whilst a less well-marked and more or less broken line was correlated with juiciness. Benson and Subba Rao (1906) also noted a relationship between greyish mid-rib and sweet stems and a white mid-rib and non-sweet stems. That dry stalks were dominant to juicy was also established by Swanson and Parker (1931).

As regards the inflorescences, the Texas workers (1929) found monofactorial inheritance for length of rachis, number of nodes to the head and number of seed branches. Short glumes are dominant to long glumes (Graham, 1916) and broad glumes to narrow (Vinall and Cron, 1921). The glume characters wrinkled to non-wrinkled and dense pubescence to glabrousness are respectively dominant and recessive (Ramanathan, 1924). Considerable work has also been done on grain colour (Graham, 1916; Vinall and Cron, 1921; Conner and Karper, 1923; Ramanathan, 1924). Sieglinger (1924) showed that three factors were responsible: *B*, for brown nucellar layer; *S*, a factor for colour in the epidermis; *R*, a factor for red in the epidermis. Swanson (1928) then showed that these factors could be extended to the structure of the seed coat. (See pages 370-371.)

Chlorophyll defects in the leaf are now well known (Conner and Karper, 1924; Karper, 1930; Karper and Conner, 1932). Rangaswami Ayyangar and Sankara Ayyar (1932) distinguished five recessive chlorophyll deficiencies—virescent, albino, pale green, lethal pale green and lingering pale green.

As regards yield, Kottur and Chavan (1928) in Bombay found correlation between yield and the following characters:—height of plant, number of nodes on the stem and length, height and thickness of the stem. Martin (1928) showed that yield was closely correlated with the number of heads per acre. Stem height was also closely correlated with yield. Patel and Patel (1929) studied a number of morphological characters and found correlation between yield and leaf area, height, thickness of stem, number of nodes, rachis length and the density of branches on the rachis. Summarizing the work done at Oklahoma (1926-1930), Harper *et al.* found that stem length and yield show little correlation, but length of seed, branches and circumference of head were strongly related. Kulkarni (1930) also found that stem length was only moderately correlated with yield, but length and breadth of ear were strongly correlated. He further found a negative correlation between yield and number of grains per gramme, and accordingly suggested sieving the grain as a means of eliminating the low-yielding strains.



Karper and Conner (1921) and Conner and Karper (1924) inbred varieties of Kaffir for seven generations. There was marked constancy in head characters from the F<sub>2</sub> generation onwards. No decrease in vigour or yield was noted. The same authors (1927) found heterosis in the F<sub>1</sub> and F<sub>2</sub> generations of varietal crosses, but in strain crosses, one only exhibited the phenomenon.

As in Maize, semi-sterility has been found in Sorghum. In some instances, it is apparently due to the structure of the glumes which prevents the flowers from opening and so produces a cleistogamous condition. Vinall (1926), however, found a case in which the sterility amounted to 96 per cent. and appeared to be due to deficiency of pollen.

Moodie and Ramsay (1929) obtained crosses between Saccharine Sorghum and Sudan Grass. When tested for hydrocyanic acid, the crosses were found to contain more than three times the amount present in the Sorghum parent.

Of greater interest was the production in 1930 (Thomas and Venkatraman) of hybrids between sugar cane and sorghum. (See sugar cane, page 353.)

## II. GRASS SORGHUMS

The term "grass sorghum" was first used by Piper to include the grass-like sorghums which are annual in habit and possess no root stocks. The most important of these types is *Sorghum sudanense*, Stapf (*Andropogon Sorghum sudanensis*), and the closely related *Andropogons* already mentioned.

*Sorghum sudanense* is an annual grass, at times behaving as a bi- or perennial. It occurs wild in certain parts of N. Africa, and has apparently been cultivated for some time in Egypt and the Sudan, where it is known locally as "Garawi".

The name "Sudan grass" was given to it on its introduction to the U.S.A.

**ROOTS.**—The root system is apparently similar to that of the cultivated sorghums.

**STEMS.**—The stems are slender and solid, up to 10 feet in height, slightly furrowed on one side, the position of the furrow alternating at each node; glabrous except at the base of the nodes where a ring of fine silky hairs occurs. Buds develop at all the nodes, those at the base developing as suckers, those above as lateral branches.

The leaves are 6 to 24 inches long by  $\frac{1}{2}$  to  $\frac{3}{4}$  inches broad. The sheaths are glabrous and split, overlapping strongly at the base, but in the lower leaves open above, about the length of the inter-node, except at the base where they tend to be longer, and at the terminal leaf-node where the sheath may be often twice as long as the intermediate sheaths. The ligule is long, membranous and pubescent. The collar is distinct with brown silky hairs on the upper face. The blades have a distinct mid-rib, white above, projecting and green below; the surface is faintly ridged below and glabrous; the base of the lower leaves is often much narrowed; those of the upper less so; the apex is acute.

**INFLORESCENCE.**—The inflorescence is an ovate panicle, erect, 6 to 14 inches long up to 10 inches wide at the base. The main rachis and branches are scabrid hairy at the nodes, the ultimate branchlet carrying fine white cilia. They are also obliquely ascending, generally whorled or sometimes solitary.

Spikelets in pairs, one sessile the other pedicelled. Sessile spikelet up to 3 lines long, lanceolate to elliptic-oblong, sub-acute. Glumes 2, the lower about 13-nerved and hairy, dorsally flattened towards the apex, the sides sharply inflexed and keeled above, rounded below; the upper smaller, 7-nerved with hyaline inflexed margins. Florets 2; the lower represented by the lemma only which is about  $2\frac{1}{2}$  lines long, hyaline, 2-nerved, ciliate, deeply bifid with a fine twisted and kneed awn in the sinus; the palea, small, delicately hyaline, ciliate, about 1 line long; lodicules 2, broad and truncate and ciliate from the apical margins; stamens 3; pistil with narrow oval ovary, 2 styles, each ending in feathery stigmas. Pedicelled spikelet narrow, about  $3\frac{1}{2}$  lines long, glabrous. Lower glume up to 13-nerved with scabrid inflexed keels on upper part; upper glume 7-nerved. Florets 2, the lower with lemma only, the upper staminate, its lemma entire, ovate hyaline, mucronulate and ciliate. Lodicules, palea and 3 stamens as in flower of sessile spikelet.

MATURE GRAIN.—The grains vary from .13 to .18 inches in length and are light reddish-brown, with occasional light-coloured or almost white ones. In outline they are more or less elliptical, flattened on one side, slightly convex on the other. On the flattened side and near its proximal end, there is a small round cork-coloured scar and on the opposite side lies the comparatively large embryo. Conspicuous delicate folds or creases of the coats may here be found. The internal structures are somewhat similar to those found in *S. vulgare*. The pericarp shows a well-defined outer epidermis, a middle parenchyma of compressed thin-walled cells, and an inner epidermis of disconnected tube cells. The testa, the product of the inner integument, consists of a single cell-layer, their outer walls thin, the radial and especially the inner walls much thickened and pigmented brown. There is a single aleurone layer, and an endosperm and embryo similar to those of *S. vulgare*.

In commercial samples the caryopses are usually enclosed by the hull (outer and inner glume). They vary from .18 to .25 inches in length and from white to red, purple and black in colour.

At the base there is usually a small portion of the rachis attached, the base of which has obviously been broken. In addition, two appendages spring from the base. One of these is the continuation of the rachis; the other is the pedicel of the infertile spikelet. The tip of both these appendages is jaggedly broken and shows no expansion. In Sudan there is no suture at the base of either the fertile or infertile spikelet. As a consequence, when the grains are threshed, the rachis segments and pedicels break at their weakest point just below the insertion of the spikelet.

Many commercial samples of Sudan grass—in particular, samples from the U.S.A.—are contaminated with the seed of Johnson grass, *S. halepense*. The seeds of this grass are very similar to Sudan grass. But in Johnson grass, there is a suture below the insertion of each spikelet. Consequently, Johnson grass seed has usually no portion of the rachis attached to the base and the two appendages end, not in a jagged point, but in a slightly expanded smooth cup. Further, the unhulled seeds are smaller and tend to be darker in colour. The hulled seeds are also smaller, with a smaller and narrower embryo and a darker colour (Hillman, 1916).

GERMINATION.—Sudan grass seeds germinate with ease at a wide range of temperatures, and without any considerable period of after-ripening. On the other hand, the closely allied Johnson grass “is markedly dormant when first matured under ordinary conditions of storage, requires a number of months for after-ripening, and even when fully after-ripened will not germinate completely except with the use of alternating temperatures in a very warm temperature range.” (Harrington, 1917.)

Harrington and Crocker (1923) have studied the structure of the seed coat in Johnson grass in relation to its delayed germination, and have also compared it structurally with Sudan grass. The following table gives the difference in the chemical composition of the coat structure of these grasses.

TABLE XXXIV.

COMPOSITION OF COAT STRUCTURES OF JOHNSON GRASS AND SUDAN GRASS CARYOPSES.

Part Examined.	Composition.	
	Johnson Grass Caryopses.	Sudan Grass Caryopses.
Aleurone layer ..	Cell walls hemicellulose.	Cell walls hemicellulose.
Inner Integument ..	Inner cell walls pure suberin, impregnated with fatty substances; fat also in cell contents.	Inner cell walls hemicellulose, somewhat suberized; much less fat than in Johnson Grass.
	Outer cell walls have very little suberin; some cellulose.	Outer cell walls hemicellulose, more suberized than inner cell walls.
Pericarp .. ..	All cell layers contain pectic substances and are suberized; a little calcium; a little cellulose; iron in outer layer.	Similar to Johnson Grass but less suberized, with pectic substances much more abundant; no iron.
	All layers swell in 2 per cent. oxalic acid and in ammonium hydrate of one-tenth commercial strength.	Swell much more than Johnson Grass in oxalic acid and ammonium hydrate solutions.
“Closing tissue” of the hilar orifice ..	Suberin and considerable oil, which comes out after 10 to 15 minutes’ warming in alcohol.	Not determined.

On the whole, the coats of Johnson grass are not so thick as those of Sudan, except at the micropylar and hilar regions, but they are less fragile, more tightly enclosed and more impermeable. As a consequence, imbibition by the embryo is restricted and probably accounts for the peculiarities in germination that occur.

**CHROMOSOME NUMBERS OF THE GENUS SORGHUM.** Kuwada (1915, 1919) first reported the haploid chromosome number of *S. vulgare* as 10. This was confirmed by Marchal (1920) and Nakajima (1931). Longley (1932) examined eight varieties and Huskins and Smith (1932) about sixteen. No deviations from

the normal number were found, except that a number of tetraploid segments and one octoploid segment were found in root tips by Huskins and Smith (1932). In one of these tetraploid cells, the chromosomes were closely paired. The same authors state that the chromosomes are small, ranging from  $1.2 \mu$  to  $3.3 \mu$  long. The chromosomes exhibit individuality, though the differences are but slight. Most of them possess median or sub-terminal attachments, and often a number have a secondary sub-terminal constriction. One chromosome pair, however (termed the A-chromosomes), is distinctive. Normally this chromosome has one long portion with a prominent sub-terminal attachment constriction, and a shorter portion united to the longer by only a fine chromatin thread. In certain forms also trabants were noted.

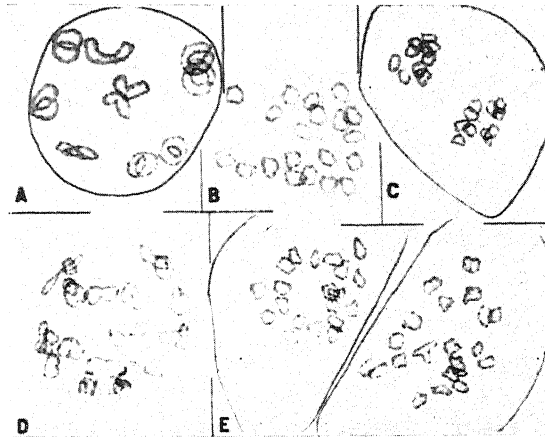


FIG. 144. Chromosomes in the pollen mother cells of *S. sudanense* and *S. halepense*.  
X 1200.

A, B and C. Diakinesis, first division anaphase and second division anaphase respectively in *S. sudanense*.

D and E. Diakinesis and second division prophase respectively in *S. halepense*. (After Longley.)

In the annual grass Sorghums, *S. virgatum*, *S. verticilliflorum*, *S. vogelianum*, *S. lanceolatum*, *S. arundinaceum* and *S. sudanense*, Huskins and Smith (1932) also found 20 chromosomes. In these species the A-chromosome was also present. Longley (1932) confirms these figures from a study of the division in the pollen mother cells of *S. Sudanense*, *S. verticilliflorum*, *S. virgatum*, *S. arundinaceum* and in addition the further species *S. drummondii* and *S. hewisonii*. It would therefore appear that all annual Sorghums have 10 haploid chromosomes, with the exception of *S. versicolor*, which has but 5 and *S. purpureo-sericeum*, which has 20.

In the perennial Johnson grass, *S. halepense*, both Huskins and Smith (1932) and Longley (1932) found the chromosome numbers to be 20 and 40. Huskins and Smith further state that in *S. halepense*, the chromosomes that are sufficiently distinct to be identified appear to be present in duplicate. This applies also

to the A-chromosome. They suggest that this indicates that *S. halepense* may be an autotetraploid, and further explains the difficulty in obtaining hybrids between this species and species with 10 chromosomes and also the marked sterility of the hybrids.

In a further paper Huskins and Smith (1934) studied the meiotic chromosomes of several species. In all the diploid species, 10 bivalents were usually found, but quadrivalent associations were also common and occasional sexivalents. In the tetraploid, *S. halepense*, 10 to 14 bivalents most frequently occurred, with the remainder of the chromosomes forming quadrivalent or higher associations. They argue that the presence of these associations, together with the occurrence of duplicate factors, is an indication of polyploidy, and suggest that 7 may be the basic chromosome number, since fewer than 7 units of association were not found.

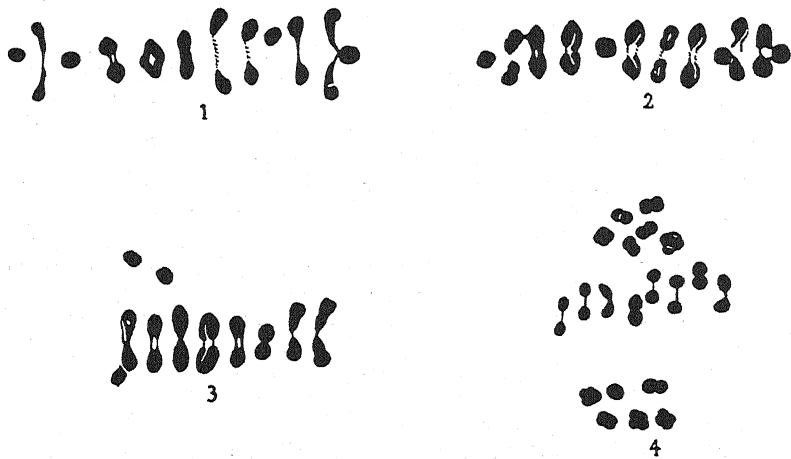


FIG. 145. Meiosis in Dakota amber Sorgo.

1 to 3. Heterotypic metaphases in 1 are  $7_{11} + 1_{111} + 3_1$ . In 2 are  $4_{11} + 2_{111} + 2_1$  plus a possible quadrivalent. In 3 are  $7_{11} + 1_{1v} + 2_1$ . In 4 are 6 chromosomes in each anaphase plate and 8 univalents dividing at the equator. (After Huskins and Smith.)

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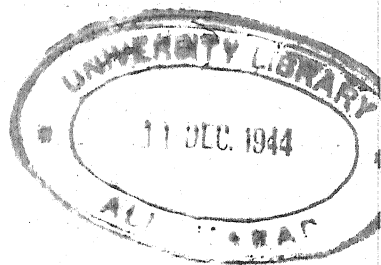
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## CHAPTER XI

### MAIZE

MAIZE, an annual cereal now known only in cultivation, is almost certainly of Tropical American origin. It is a markedly variable plant and can best be described under the comprehensive name given it by Linnaeus, *Zea Mays*.

ROOTS.—The roots are fibrous and of three types.

1. SEMINAL ROOTS.—The primary seminal root develops from the radicle of the embryo. It appears early and after growing to a considerable length, branches. The secondary seminal roots are typically 3 in number—a pair which develop right and left of the median plane at a point slightly above the insertion of the scutellum ; and a third which develops opposite the scutellum and somewhat above the point of insertion of the epiblast root in the wheat. Owing to their position, the median pair at first grow upward between the scutellum and the axis, thereafter turning sharply downwards.

Variation is frequent. An extra root may form above the insertion of the median pair, and also above the epiblast root. Each member of the median pair may be paired, as also the epiblast root. Smith and Walworth (1926) found the number of secondary seminal roots to vary from 0 to 10. The following table gives the average number recorded by them in eight varieties.

TABLE XXXV.

NUMBER OF ROOTLETS IN MAIZE SEEDLINGS.

(Data from Smith and Walworth.)

Variety.	Mean number of rootlets.		Standard deviation.	
Reid's Yellow Dent .. .. .	3.08	.04	0.55	.03
Riley's Favourite .. .. .	3.22	.04	0.46	.03
Champion White Pearl .. .. .	3.33	.04	0.46	.03
Leaming .. .. .	3.29	.04	0.48	.03
Silvermine .. .. .	3.38	.04	0.36	.03
Boone County White .. .. .	3.18	.03	0.36	.02
Golden Eagle .. .. .	3.40	.03	0.45	.03
Western Ploughman .. .. .	3.55	.05	0.51	.03

They conclude that kernels of an individual ear may show a wide range of variability in root numbers ; that individual ears possess characteristic tendencies in this respect ; and that varieties show small but characteristic differences.

In the sweet corns, however, the primary root system usually consists of a single much branched root.

As regards the duration of the seminal roots, the evidence now points to the

conclusion that they function throughout the life of the plant. They have been traced by the author in plants up to 5 weeks old. Three such roots running nearly horizontally are distinguishable in Weaver's Figure 7 (*Roots of Crop Plants*, Fig. 7). Later, the seminal roots may penetrate to very considerable depths. Except for the last few inches, they are always profusely branched.

2. ADVENTITIOUS ROOTS.—The adventitious roots develop from the nodes near ground level. They are said to form about an inch below the surface no matter how deep the planting. Not more than four develop in whorls

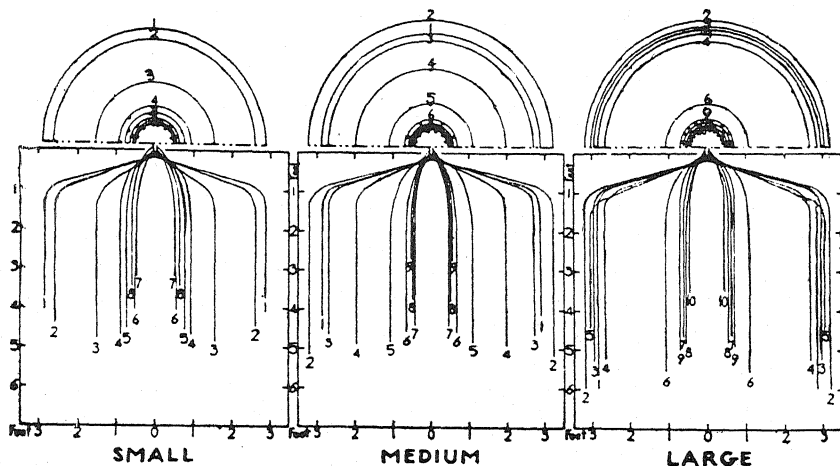


FIG. 146.—Diagrams of adventitious root systems of small, medium and large types of maize at maturity. In the lower portion the lines drawn from the base of the stalk show the average spread and depth of roots from individual nodes. The number at the end of each line indicates the node from which the root arose. The upper portion of the diagram indicates the number and distribution of the roots on one side of the plant only. The radii of the various arcs correspond to the average spread of the roots from the respective nodes whose position is indicated by the numeral just above or on the arc. The number and approximate location of the roots for individual nodes is shown by the small circles distributed along the corresponding arcs. (After Weihing.)

at the succeeding nodes which at the base of the stem are crowded together. Weaver *et al.* (1919) and Weaver (1926) have described the development in detail.

The early-formed adventitious roots (in plants up to 5 weeks old) are 10 to 15 in number. They run almost parallel to the soil surface or at a slight angle and are confined almost entirely to the surface foot of the soil. They vary in length from .1 to 2.6 feet, and are branched profusely to near the apices. In older plants, the above roots and certain newer ones from the same nodes, spread laterally for a distance of 2 to 4 feet; they then generally turn sharply downwards. They penetrate the soil from 1.5 to 4.6 feet. The younger roots are more bunched, the spread being only some 10 to 20 inches. They grow almost vertically downwards, the maximum depth reached being 4 to 7 feet.

All the roots, especially those near the surface, are much branched. The colour is either brown or white depending on the age. In mature plants,

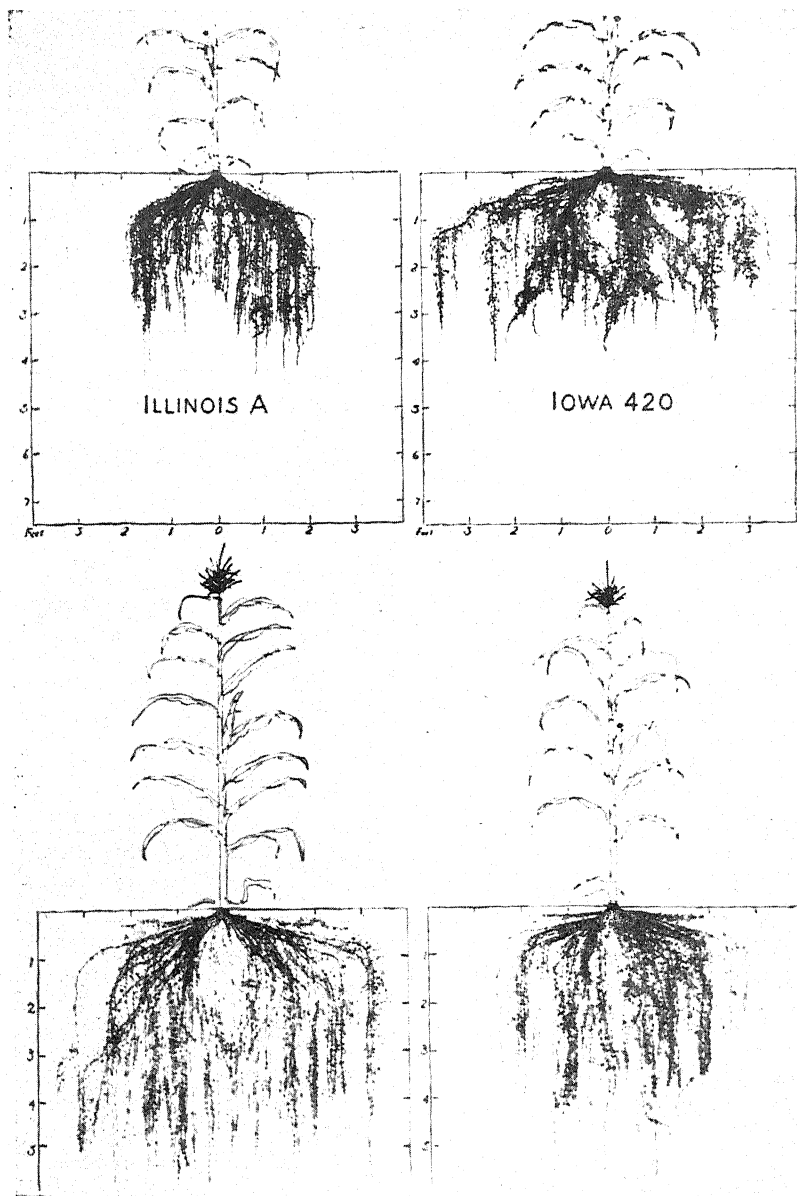


FIG. 147.—Relative root development in selfed lines of maize and their  $F_1$  and  $F_2$  hybrids.

1. A representative plant from selfed Illinois.
2. The same from Iowa.
3. The  $F_1$  hybrid of the above.
4. The  $F_2$  hybrid.

Approximately 25 per cent. of the roots are shown. (After Kiesselbach and Weihing.)

the shallower roots are little altered. Some spread horizontally at a slight angle for varying distances (a few inches to .3 to 7 feet) and then turn downwards abruptly or with a gentle curve, continuing in this direction for distances varying up to 3 feet. All these are much branched to the second and third order. The more vertically growing and in general the later-formed roots are 20 to 35 in number. They grow straight downwards or obliquely outward for some 2 feet. Others are much longer; and may reach a depth of 7 feet and more. All are profusely branched.

In general, maize appears to have an average lateral spread of 3.5 feet, and a penetration of from 5 to a maximum of 8 feet. Sweet corn has a similar but smaller root system. (Weaver, 1919; 1926.)

Varietal and heritable differences also exist both as regards the extent of the root system and as regards susceptibility to fungus disease. Thus, Weihing (1935) studied at Lincoln, Nebraska, a number of representative varieties which could be grouped on the basis of size into small, medium and large vegetative types. In these three classes the mean values for certain of the differential characters used to separate them were as follows:—(a) Heights of 55, 87 and 92 inches; (b) leaf areas of 658, 1,412 and 1,747 square inches; (c) moisture-free fodder weights of 248, 380 and 622 grams; (d) periods from planting to ripening of 88, 112 and 129 days; (d) number of nodes bearing functional main roots of 8, 9 and 10 respectively.

In general, the size of the secondary root system increased markedly with the increase of the parts above ground. On the basis of the small type, the medium and large types possessed respectively (a) 33 and 50 per cent. greater maximum spread; (b) 9 and 10 per cent. deeper maximum penetration and 15 and 23 per cent. greater average depth of penetration; (c) 42 and 65 per cent. more functional main roots; (d) 22 and 92 per cent. greater combined length of main roots per plant; (e) 115 and 311 per cent. greater root weight; (f) 86 and 268 per cent. greater root volume; and (g) 10 and 29 per cent. larger diameter of main roots. These differences are illustrated graphically in Fig. 146. Similarly, Kiesselbach and Weihing (1935) compared the root systems of two standard inbred strains, their F<sub>1</sub> and F<sub>2</sub> progeny. The inbred strains exhibited characteristic differences and the F<sub>1</sub> generation distinct heterosis. The results obtained on crossing Illinois A and Iowa 420 are represented in Figure 147. Further the weaker rooted types are more liable to lodge and give lower yields. (Holbert and Koehler, 1924; Holbert *et al.*, 1924.) Soil conditions markedly influence the development. A moist, warm, rich soil tends to develop a more superficial system, and irrigation produces marked effects (Weaver, 1926; Jean and Weaver, 1924).

3. BRACE OR PROP ROOTS.—At the time of rapid elongation of the stem, several of the nodes above the ground level may send out whorls of brace or prop roots. These roots are thicker than the normal and often deeply pigmented. Their surface is somewhat mucilaginous, with the epidermis silicified and the sclerenchyma well developed. On entering the soil they behave as ordinary roots.

ANATOMY OF THE ROOT.—In a longitudinal section of the apex of the seminal root, we find on the outside, the root cap, a covering layer of somewhat elongated parenchymatous cells, whose surface is constantly being worn away, but whose mass is kept constant by additions on the inner face from the meristem.

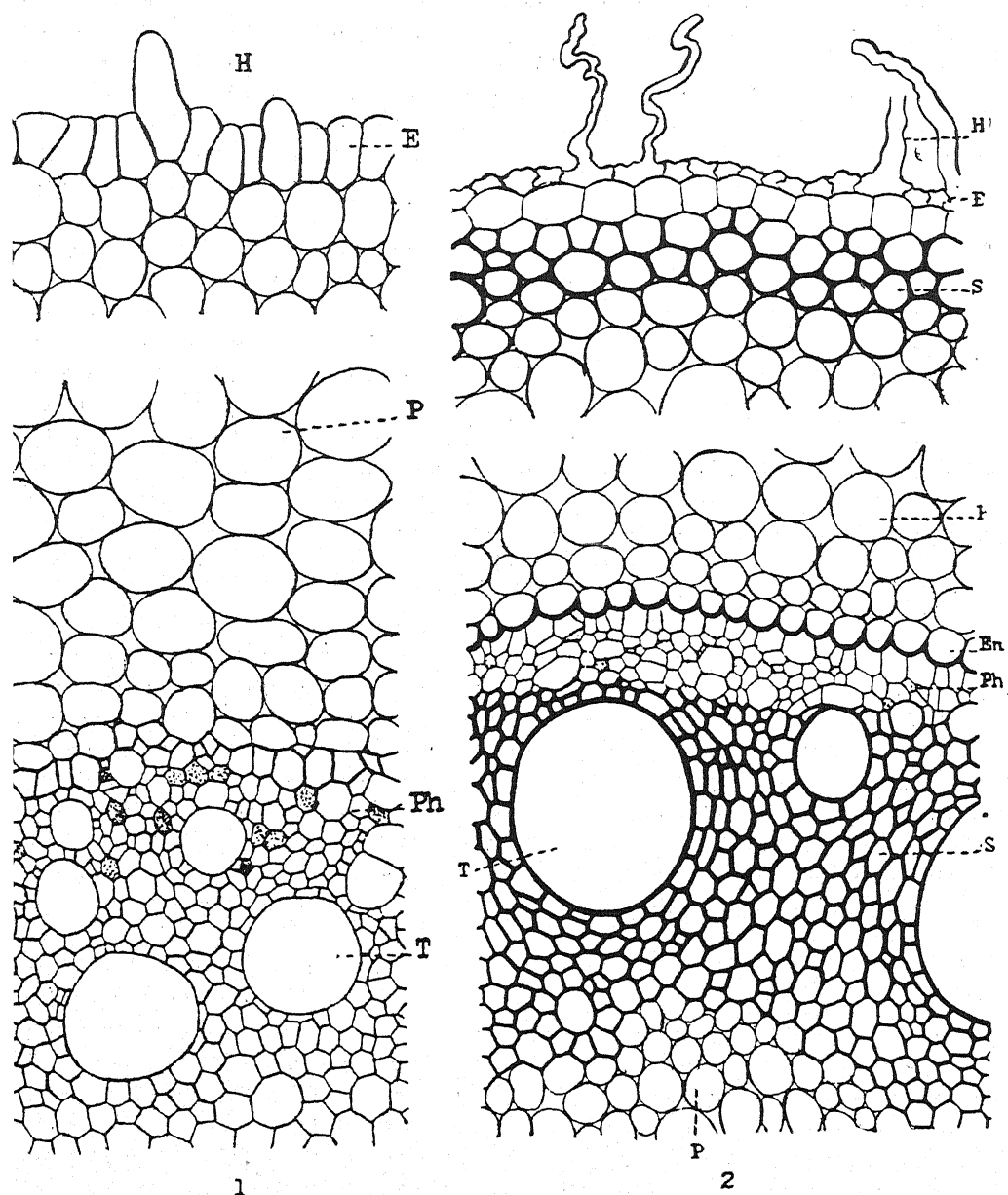


FIG. 148.—1, Portions of cross-section of a young root. *H*, root hair; *E*, epidermis; *P*, parenchyma; *Ph*, phloem; *T*, trachea. 2, Portions of cross-section of an old root. *H*, root hair; *E*, epidermis; *S*, sclerenchyma; *P*, parenchyma; *En*, endodermis; *Ph*, phloem; *T*, trachea. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

This meristem occupies the apex and passing upwards differentiates into the periblem and plerome. The plerome later resolves itself into : (1) the piliferous layer on the outside, (2) a cortex of several layers and (3) the endodermis, the innermost layer of the cortex. The plerome becomes the central cylinder. Its outermost layer in contact with the endodermis is the pericycle. Some distance within, 6 to 8 cells are recognizable owing to their size. As they pass upwards they differentiate into 6 (6 to 8) primary vessels. Between and behind these cells, smaller vessels are also differentiated. Between each of these is the scanty phloem. A section, a few centimetres from the apex, shows the same tissues ; (1) the cortex bounded by the piliferous layer to the exterior and the endodermis to the interior. This endodermis is thickened on its inner and radial walls. (2) The central cylinder. The outermost layer is the pericycle, a continuous band of small cells adjoining the endodermis. Beyond this are alternate bands of xylem and phloem, the number varying somewhat. The phloem consists of 3 to 4 sieve-tubes ; the xylem of small vessels, with annular or spiral thickening ; and the centripetally-formed vessels which develop later and are generally wider and pitted. The interior is filled with conjunctive tissue. In this tissue, however, the 6 to 8 large vessels already referred to, occur. They lie opposite certain of the xylem strands, and at first sight appear to be the last-formed vessels of the centripetal wood. This, however, is not the case. The large vessels are primary and formed almost simultaneously with the protoxylem.

**STEMS.**—The length of the stems varies from scarcely 3 feet up to 15 feet. A number of true recessive dwarf forms has also been described. They are clearly marked into nodes and inter-nodes. At the base of the nodes the stem is thickened. There, too, is found the meristematic tissue which is responsible for the growth in length and to a limited extent, thickness. In a young seedling, .5 to 10 inches high, all the parts are differentiated. The lower inter-nodes are thin and short ; the upper longer but thicker, becoming gradually thinner again upwards. The result is a stem tapering gradually upwards to the tassel, abruptly downwards to the cotyledon. Both nodes and inter-nodes are solid. On the side next the leaf the stems are furrowed, the position of the furrow alternating at each node. The last node ends in the tassel.

**TILLERS AND BRANCHES.**—There is a considerable difference in the branching of maize as compared with wheat. In wheat the tillers develop at the lower nodes only ; in maize a bud forms in the axil of each leaf. Those at the lowest nodes (1, 2 and 3) generally fail to develop. The uppermost are reduced. The buds near ground level may grow to form tillers as in wheat, but their number is greatly limited, though influenced in much the same way as in wheat. The buds at higher levels especially those in the axils of the larger leaves form the " pistillate branches ", whose structure we shall consider later. The number tends to vary with the variety and the spacing.

**ANATOMY OF THE STEM.**—The stem of the maize is solid, both at the nodes and inter-nodes. It shows the following structures.

The cells of the epidermis, like those of the leaf, are elongated, with somewhat sinuous walls, and hardened with deposits of silica. On the more exposed parts parallel lines of stomata occur. Beneath the epidermis there lies a continuous band of sclerenchyma, interrupted at intervals by the stomata. These open into large



air-spaces, bounded internally by thin-walled parenchymatous cells containing chlorophyll. There is no hypodermis equivalent to that of the wheat. A little further inwards the solid parenchyma of the stem is traversed by isolated fibro-vascular bundles, whose number though large is variable, becoming less numerous and less definitely orientated towards the centre.

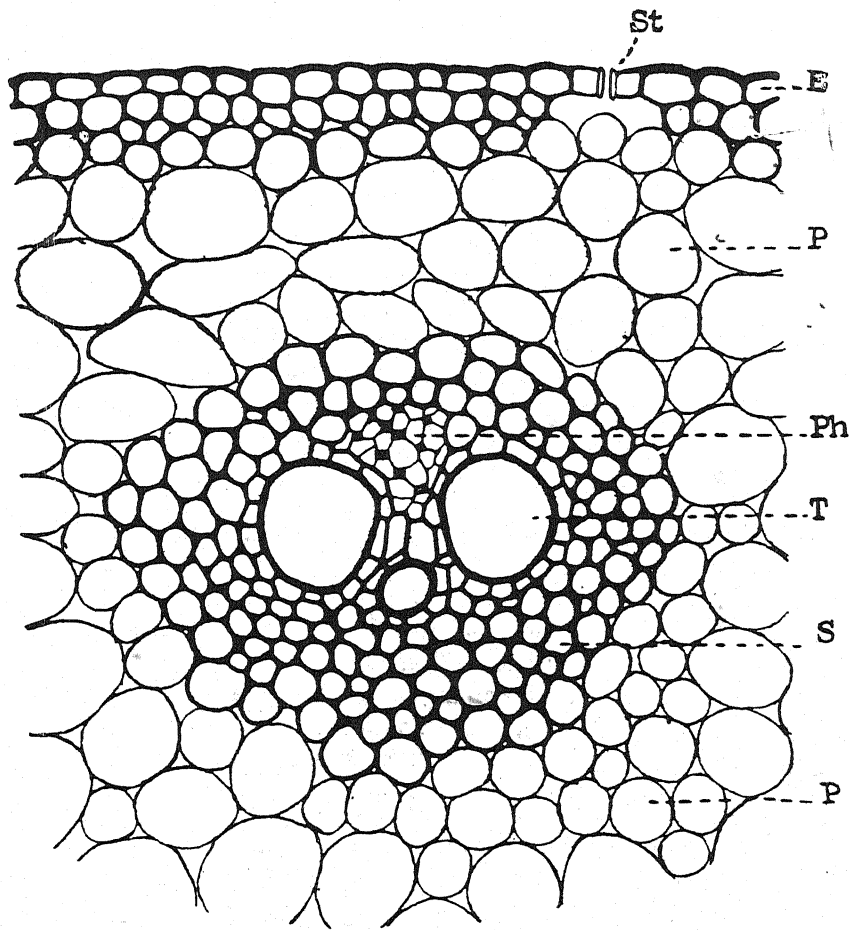


FIG. 149.—Transverse section of stem showing bundle near the periphery.

*E*, epidermis; *St*, stoma; *P*, parenchyma; *Ph*, phloem; *T*, trachea; *S*, sclerenchyma; *P*, pith. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

Each bundle is of the closed collateral type, with the xylem to the interior and the phloem to the exterior. The chief vessels of the xylem have the usual V-shape. At the apex of the V one or two annular or spiral vessels form the protoxylem. They abut on a distinct air-space. On each limb of the V, a large pitted vessel occurs. These are connected to one another and to the protoxylem by small tracheids. Between and beyond the open limb of the V is the phloem.

It is composed of sieve-tubes and their companion cells, all more or less regularly arranged. Surrounding the bundle there is a sheath of several layers of fibrous stereome.

*The nodal complex.*—At the nodes, the bundles form a complex of intertwining bundles. Strasburger (1891) stated that the longest leaf trace passes through 6 inter-nodes. Evans, 1928, however, found that no bundle passed through more than 3 nodes without branching. At the point of entry into the node, a bundle enlarges and may become deflected to one side or the other, whilst producing a

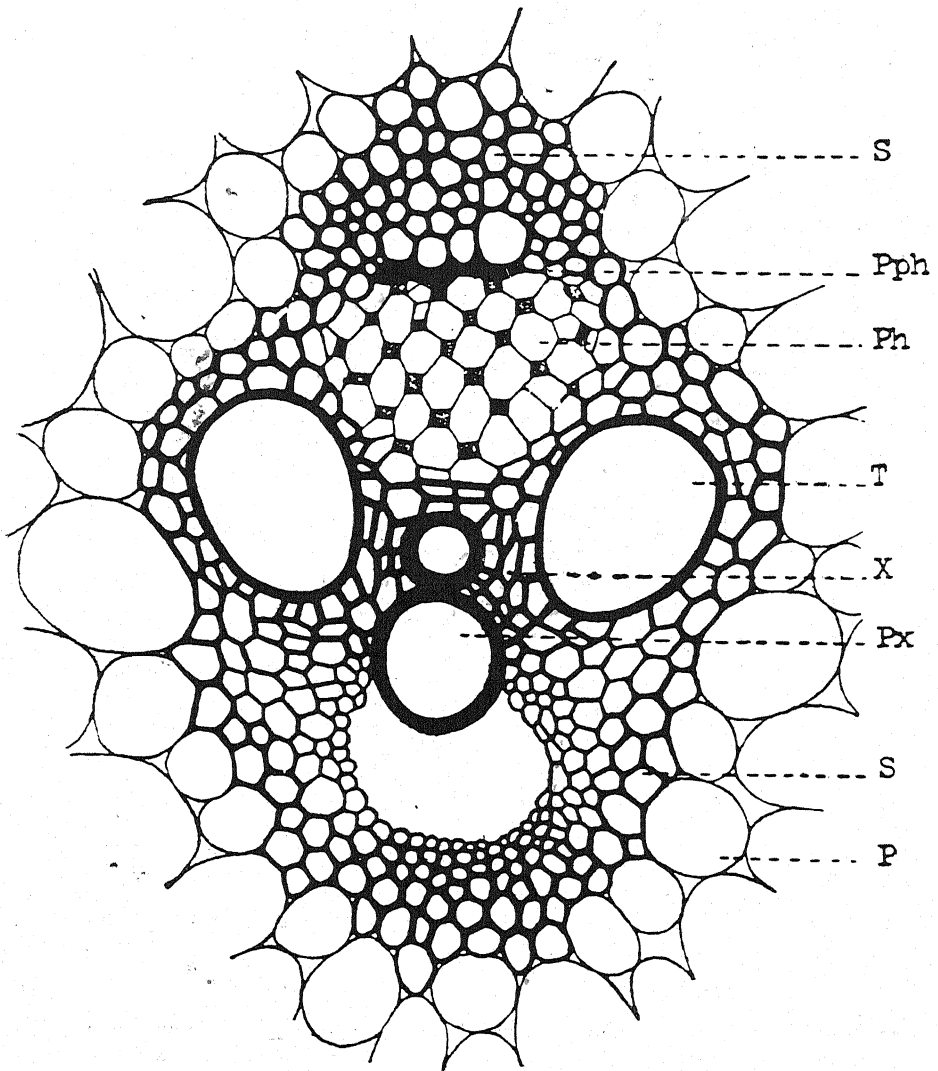


FIG. 150.—Section of a well-developed, centrally located vascular bundle. *S*, sclerenchyma; *Pph*, protophloem; *Ph*, phloem; *T*, trachea of the xylem; *X*, tracheids; *Px*, protoxylem; *P*, parenchyma. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

variable number of branches. The smaller peripheral branches may also give off a series of nodal branches which loop round the neighbouring vascular strands. These branches, together with the branches from the larger bundles, form the complicated vascular network which characterizes the nodal situation.

The origin of the nodal complex, however, is very difficult to understand, and conflicting views have been advanced.

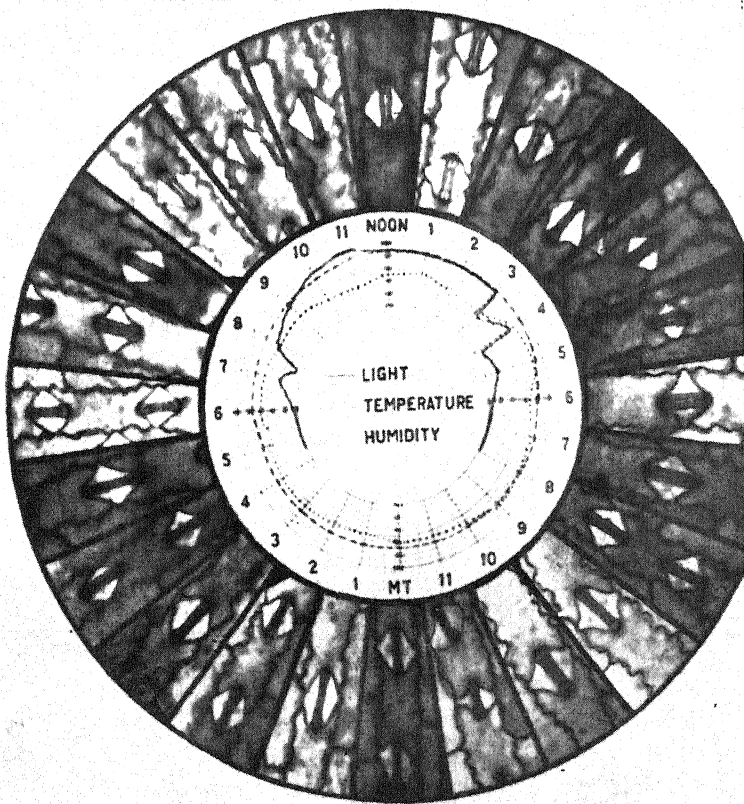


FIG. 151.—Stomatal movements throughout a 24-hour period. (After Loftfield.)

**LEAVES.**—As in wheat, the leaf in maize may show several modifications, 1/ the cotyledon, 2/ the coleoptile, 3/ the foliage leaves, 4/ the prophylls, 5/ the husks and 6/ the bracts of the inflorescence. The foliage leaves and prophylls will here alone be dealt with.

**FOLIAGE LEAVES.**—The foliage leaves vary in number from 8 to 20 and are arranged alternately with a divergence of 180 degrees. Each possesses the four parts, sheath, blade, ligule, and auricles.

a. *Sheath.*—The sheath is attached to the node and encircles the inter-node for a variable distance. It is entire below and split above. The surface is glabrous or pubescent; the margins glabrous below, often becoming strongly fringed with hairs above.

b. *Blade*.—The blade is continuous with the sheath. It is a thin, flat almost ribbon-like structure with an acute apex. Along the edges and at the base, it may be thrown into a number of folds. A firm mid-rib, yellowish in colour, traverses the entire length. It is composed mainly of sclerenchyma with a core of parenchyma and contains several fibro-vascular strands. Numerous smaller veins run parallel to the mid-rib. They anastomose somewhat at the base and at the apex, and, as in wheat, vascular strands afford cross-connection. The surface is slightly ribbed, and either glabrous or pubescent.

Various shades of purple to brown may develop in certain of the vegetative parts of the plant such as the leaves, husks, stalks and tassels. Three fundamental factors are concerned :—*A*, the factor necessary for basic anthocyan colour as in the aleurone ; *P*<sub>1</sub>, which converts the red of *A* to purple and *B*, which gives rise to a brown flavone pigment. Their interaction accordingly gives rise to the following colours ; *ABP*<sub>1</sub>, purple ; *ABp*<sub>1</sub>, sun-red ; *AbP*<sub>1</sub>, dilute purple ; *Abp*<sub>1</sub>, dilute sun-red ; *aBP*<sub>1</sub>, brown ; other combinations green. Modifying factors may also influence the expression (Emerson, 1921). Certain of these factors also interact with the factors for aleurone, pericarp and silk colours (Emerson, 1921 ; Anderson, 1921 ; Anderson and Emerson, 1923 ; Anderson, 1924 ; Meyers, 1927):

Two further allelomorphs of *A* have since been discovered, *Ab* and *ap* (Emerson and Anderson, 1932). The 4 allelomorphs of *A* form accordingly a complex series whose inter-relations are indicated in the following table :—

TABLE XXXVI.

RELATIONS OF THE *a*<sub>1</sub> ALLELOMORPHS TO ALEURONE, PLANT, PERICARP AND SILK COLOUR.\*  
(Data from Emerson and Anderson.)

Allelomorphs of <i>A</i> .	Aleurone Colour with <i>CRP</i> <sub>r</sub> .	Plant Colour		Pericarp Colour		Silk Colour with <i>Psm</i> .
		with <i>BP</i> <sub>1</sub> .	with <i>Bpl</i> .	with <i>Plr</i> <sup>ch</sup> .	with <i>P</i> .	
<i>A</i> <sup>1</sup> <i>A</i> <sup>1</sup> ..	Strong purple	Purple	Sun red	Cherry	Red	Salmon
<i>A</i> <sup>1</sup> <i>a</i> <sup>1</sup> ..	Strong purple	Purple	Sun red	Cherry	Red	Salmon
<i>A</i> <sup>1</sup> <i>Ab</i> <sup>1</sup> ..	Strong purple	Purple	Sun red	(Cherry)	Brown	Green
<i>A</i> <sup>1</sup> <i>a</i> <sup>b1</sup> ..	Strong purple	Purple	Sun red	Cherry	Brown	(Green)
<i>A</i> <sup>b1</sup> <i>A</i> <sup>b1</sup> ..	Strong purple	Purple	Sun red	(Cherry)	Brown	Green
<i>A</i> <sup>b1</sup> <i>a</i> <sup>b1</sup> ..	(Strong purple)	(Purple)	(Sun red)	(Cherry)	(Brown)	(Green ?)
<i>A</i> <sup>b1</sup> <i>a</i> <sup>1</sup> ..	Strong purple	Purple	Sun red	(Cherry)	Brown	(Green ?)
<i>a</i> <sup>b1</sup> <i>a</i> <sup>b1</sup> ..	Pale purple	Reddish-brown	Green	Brown	Brown	(Green ?)
<i>a</i> <sup>b1</sup> <i>a</i> <sup>1</sup> ..	Pale purple	Reddish-brown	Green	Brown	Brown	(Green ?)
<i>a</i> <sup>1</sup> <i>a</i> <sup>1</sup> ..	White	Brown	Green	Brown	Brown	Green

\*Combinations not tested directly are given in parenthesis.

Abnormal leaf colours due to defective chlorophyll are fairly common. Such chlorophyll abnormalities are of two types—those which appear in the seedling and those which develop as the plants mature.

Of the seedlings, three main forms exist, white, virescent white, and yellow. The white forms are true albinos; the virescent whites gradually turn greenish, especially at the leaf tips, and vary from seedlings which develop some chlorophyll at ordinary temperatures to seedlings which remain white at low temperatures but become green at normal temperatures.

A very large number of factors have now been shown to be responsible and owing to their interaction a wide range of expression occurs.

TABLE XXXVII.

## CHLOROPHYLL DEFICIENCIES IN MAIZE.

(Data from Phipps, 1929.)

Character.							Number of factors concerned.
White seedlings, $w_1$ to $w_{11}$	..	..	..	..	..	..	11
Dominant white seedlings	..	..	..	..	..	..	1
Xantha seedlings, $xn_1$ , $xn_2$	..	..	..	..	..	..	2
Pale green seedlings, $pg_1$ to $pg_5$	..	..	..	..	..	..	5
Yellow-green seedlings, $yg$	..	..	..	..	..	..	2
Virescent seedlings, $v_1$ to $v_{20}$	..	..	..	..	..	..	20
Yellow white seedlings $m_1$ , $m_2$	..	..	..	..	..	..	2
Ghost seedlings, $gh$	..	..	..	..	..	..	1
Golden, $g_1$ , $g_2$	..	..	..	..	..	..	2
White-base leaf, $wl$	..	..	..	..	..	..	1
Argentia, $ar$	..	..	..	..	..	..	1
Fine-striped, $f_1$ , $f_2$	..	..	..	..	..	..	2
Fine-streaked, $fi$	..	..	..	..	..	..	1
Lineate, $li$	..	..	..	..	..	..	2
Japonica-striped, $j$	..	..	..	..	..	..	1
Green-striped, $gs$	..	..	..	..	..	..	1
Maternally inherited striping	..	..	..	..	..	..	—
Ioap striping	..	..	..	..	..	..	1
Zebra-striped leaves, $zb_1$ , $zb_2$	..	..	..	..	..	..	2
White sheath	..	..	..	..	..	..	1
Piebald seedlings, $pb_1$ to $pb_4$	..	..	..	..	..	..	4
Polka-dot leaves, $pk$	..	..	..	..	..	..	1
Blotch leaf, $bl$	..	..	..	..	..	..	1
							65

The normal green plant contains dominant allelomorphs to all these abnormalities, which are essentially lethal.

In the mature plant, golden, green-striped, Japonica-leaved, fine-striped and spotted forms, etc., have been described. They appear to be recessive to the normal green. (Emerson, 1912; Lindstrom, 1918; 1921, 1924, 1925; Demerec, 1923, 1924 b; Phipps, 1929.)

c. *Ligule*.—Except in certain types isolated by inbreeding (Emerson, 1912), the ligule is present as a membranous outgrowth from the epidermis at the junction

of blade and sheath. It is colourless and closely invests the stem, and is approximately a quarter of an inch long.

d. *Auricles*.—The base of the leaf contracts and then expands as 2 lateral lobes, generally termed the auricles. Whether these really correspond to the auricles of the wheat seems doubtful. They are absent or poorly developed in certain genetic types.

PROPHYLLS.—The first-formed leaf of each branch, including the pistillate, is much modified and known as the prophyllum. It is a sheath-like structure with two prominent keels. Within each keel there is a single vascular bundle. Certain authors regard the prophyll as a pair of congenitally fused leaves, each keel corresponding to the mid-rib of one of the constituent members. Others have interpreted it as a single leaf reduced to its sheath, the keeling being the mechanical result of pressure during development. In Maize, however, 2 buds may form in the axil of the prophyllum and Collins (1924) considers that this fact lends support to the fusion hypothesis.

ANATOMY OF THE LEAF.—*Epidermis*.—The epidermis is continuous except where broken by the stomata. Its cells are elongated with sinuous margins. Short square cells are at times intercalated. The lower surface is flat and glabrous with the stomata in parallel bands. The upper surface is almost flat. At regular intervals, parallel rows of motor cells are found. There are usually three such rows, flanked on either side by one or two hairs. These hairs curve over as if to protect the turgid cells. Between each series of motor cells there occur:—1/ a parallel series of cells without stomata, 2/ a similar stomatal series, 3/ a series without stomata, 4/ a second stomatal series, 5/ a third series without stomata. Such perfect regularity, however, is not always found.

*Stomata*.—The stomata are almost identical to those of the wheat. They are somewhat more numerous on the lower face (60,000 to 100,000 per inch on the lower surface compared with 50,000 to 60,000 on the upper).

*Parenchyma*.—The parenchyma consists of large somewhat irregularly-shaped cells with small inter-spaces. Practically all are capable of assimilation, except at the mid-rib, where the cells are almost devoid of chloróphyll. Each stoma opens into a single large air-space.

*Fibro-vascular bundles*.—As in wheat, three types occur—the major bundles, the minor bundles and the transverse veins. The major bundles, except in the tissue of the mid-rib, are girdered above and below. In the mid-rib they are girdered below only and are of two sizes. The minor bundles are comparatively small and are never girdered. The bundles are collateral, the xylem above, the phloem below. The outer sheath is obvious but not the inner. In the major bundles it consists of large cells with fairly thick walls and no chlorophyll content. In the minor bundles, the sheath cells are thin-walled with large prominent chloroplasts. In the major bundles there are usually 2 vessels above, with annular or spiral thickenings; below and on either side of these, there is a single large vessel with pits. The remainder of the tissue is similar to that of the stem bundles. The minor bundles tend to be simplified, often only a single vessel being found. The distribution and structure of the bundles is seen in Figures 152 and 153.

*Sclerenchyma*.—Above and below the major bundles of the blade are the so-called "Girders", strands of sclerenchymatous fibres. Their lumen is almost

obliterated by the thickening of the walls. At times these strands, especially on the upper face, project as low ridges. The major bundles of the mid-rib are also girdered, but only to the lower surface. There, too, a band of sclerenchyma occurs just below the upper surface. The margins of the leaf are also strongly reinforced with a stout strand of sclerenchyma.

*Sheath*.—The structure of the sheath is somewhat similar to that of the blade. The stomata are, however, fewer, and the assimilating tissue less.

**INFLORESCENCE**.—Maize is monoecious but diclinous. That is to say, the stamens and pistils are borne on separate inflorescences, but on the same individual plant. The staminate flowers are carried terminally on the so-called "tassel"; the pistillate on the "ear", terminating a short lateral branch.

**I. STAMINATE INFLORESCENCE**.—The "tassel" is a terminal panicle. The central axis is continuous with the main axis of the stem, and carries—especially below—a variable number of spirally arranged lateral branches. On the central

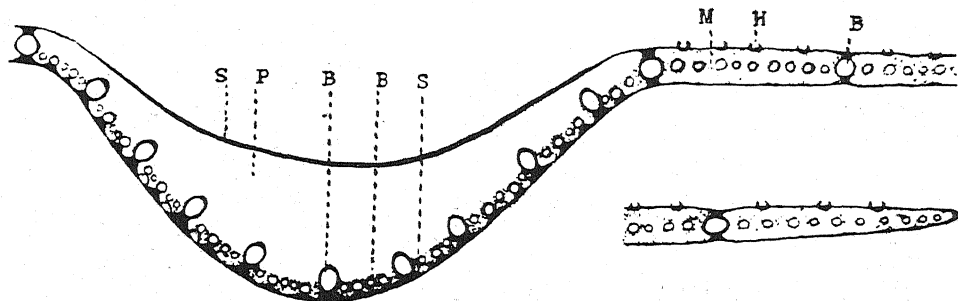


FIG. 152.—Diagram of a cross-section of the blade of the leaf. *S*, sclerenchyma; *P*, parenchyma; *B*, vascular bundle; *M*, mesophyll; *H*, hygroscopic cells with adjacent hairs. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

axis, the spikelets are arranged in rows, varying in number from 4 to 11. Each row consists of a pair of spikelets, one sessile, the other pedicellate. On the laterals, the spikelets, also in pairs, are reduced to two rows.

Marked variation in the development of the "tassel" is met with. It may be reduced to the central axis, or it may carry many laterals. In some the axes are thick and rigid, the tassel being then erect; in others, the axes are thin and more flexible, giving a drooping appearance to the whole. In the "ramosa" type, the central axis is branched almost to the apex.

**2. PISTILLATE INFLORESCENCE**.—The pistillate inflorescence terminates a short lateral branch, which develops from a bud in the axil of one of the larger foliage leaves. Sometimes 2, very rarely 3, buds may develop. The developmental succession is then usually from above downwards.

In structure, this branch is somewhat similar to the main shoot. All its inter-nodes are short, but the uppermost is the shortest, the others becoming progressively longer as you pass downwards. The leaf at the basal node is the prophyllum; the other leaves constitute the "husk", overlapping and protecting the terminal "ear".

Each envelope of the husk is a modified leaf. The sheath in each case is well developed ; the blade is reduced, becoming more and more so as you pass upwards. The ligule is visible on the lower ones, but is a mere trace or absent above. Secondary ear buds may form in the axil of each.

The " ear " is a modified spike and consists of a thickened central axis, the " cob ", carrying a series of paired spikelets in longitudinal rows. (Montgomery, 1906.)

As each row of paired spikelets develops 2 grains (one from each spikelet of the pair), the regular occurrence of an even number of rows of grains is inevitable.

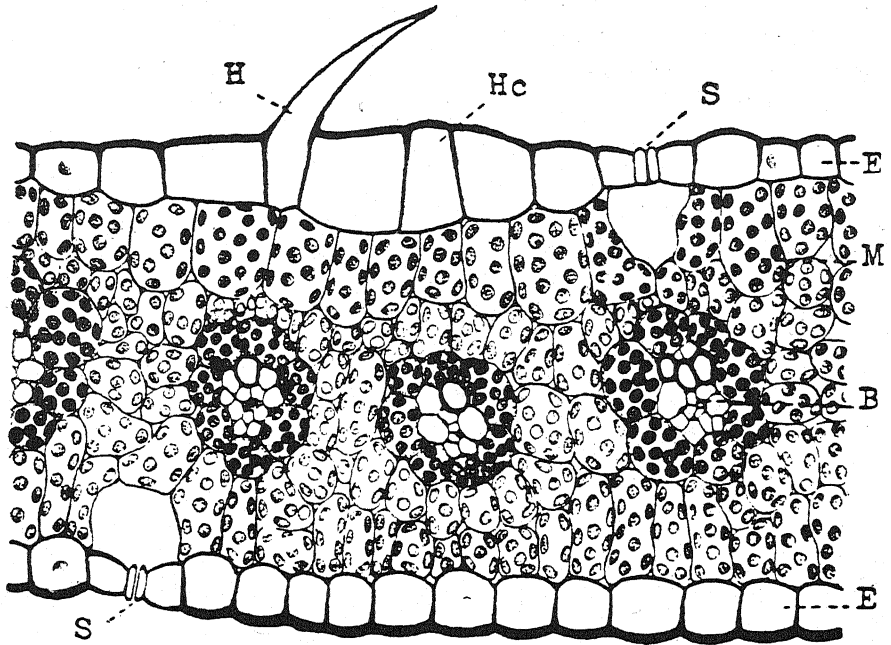


FIG. 153.—Cross-section of blade of leaf. *H*, a leaf hair (trichome) ; *Hc*, hygroscopic cell ; *S*, stoma ; *E*, epidermis ; *M*, mesophyll ; *B*, vascular bundle. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

The number of rows of paired spikelets is very varied. Two rows (producing a 4-rowed ear) are rare ; 3 rows, which would produce a 6-rowed ear, are practically unknown ; 4 rows, producing an 8-rowed ear are common ; and so up to 15 (or more) rows, producing a 30- (or more) rowed ear.

The axis or cob, which tapers gently to a dome-shaped apex, has the structure of the stem, but the inter-nodes are so close together that they are indistinguishable. The centre is filled with a white pith, and the very numerous fibro-vascular bundles form a compact network in the peripheral woody sclerenchyma. Its colour varies from red to orange, through variegated to white. Cob and pericarp colours are inter-related.

**STAMINATE SPIKELETS.**—The paired staminate spikelets are identical except for the fact that one is sessile and the other is borne on a short stalk.



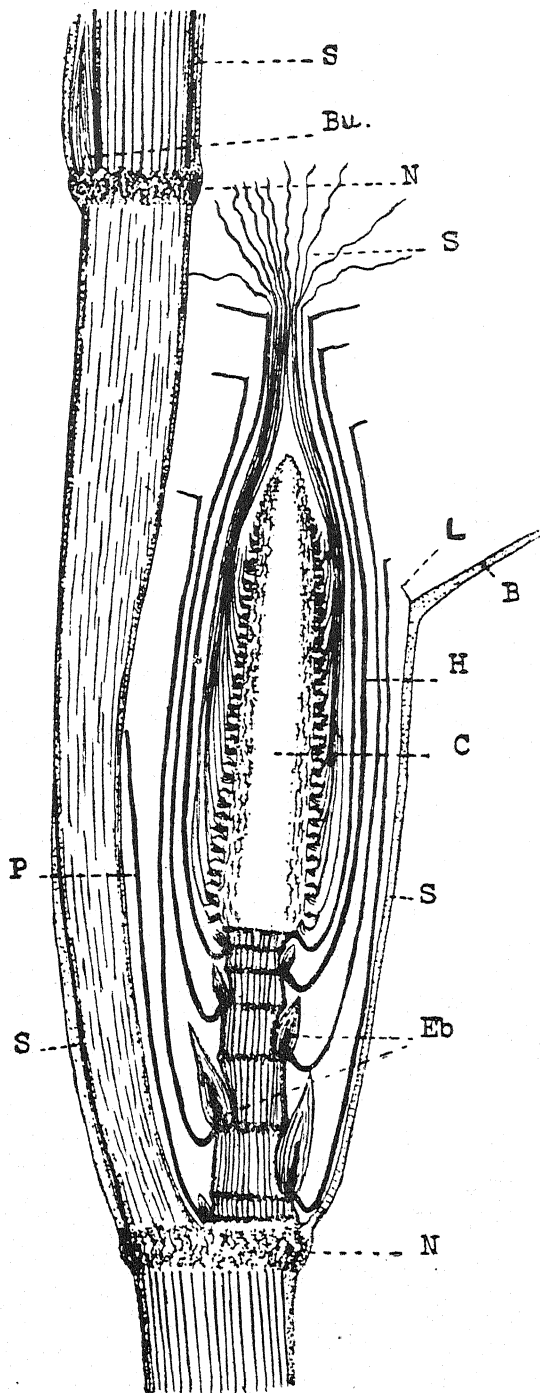


FIG. 154.—Diagram of longitudinal section of ear-bearing branch.

S, leaf sheath; Bu, axillary bud, an undeveloped ear-bearing branch; N, node of the main axis; S, silks exposed beyond the ends of the husks; L, ligule; B, leaf blade; H, husk of the ear, a greatly enlarged leaf sheath; C, cob of the ear; Eb, secondary ear buds; P, prophyllum. (After Weatherwax, *The Story of the Maize Plant*, by permission of the Chicago University Press.)

At the base of each is a pair of glumes. They are slightly longer than the spikelet and almost equal in size; glabrous, 7- to 12-nerved, except at the margins and the apex where there are fine short hairs. The outer or lower glume slightly overlaps the inner or upper; its apex is also more tapering than that of the inner.

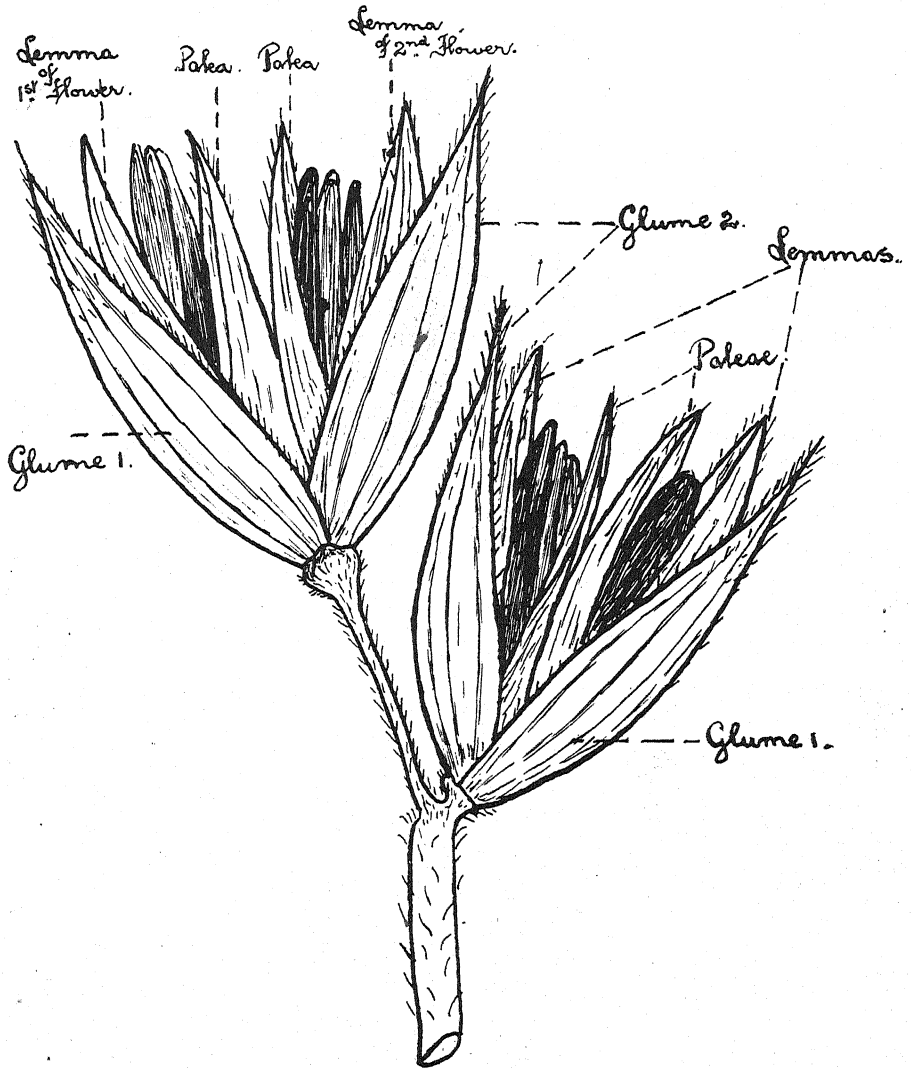


FIG. 155.—Paired Staminate Spikelets of Maize, the one sessile, the other pedicelled.

Within the glumes there are 2 flowers, both staminate and borne on a much shortened rachilla.

STRUCTURE OF THE FLOWER.—Each flower possesses an outer bract, the lemma, and an inner, the palea. The lemma is more or less oval, concave, 3-nerved and glabrous except at the upper margins and at the somewhat rounded apex

The palea, inserted opposite the lemma, is thin and membranous, 2-nerved, almost flat and with inturned margins. The palea of the upper flower is larger than the lemma; in the lower flower the lemma is larger than the palea.

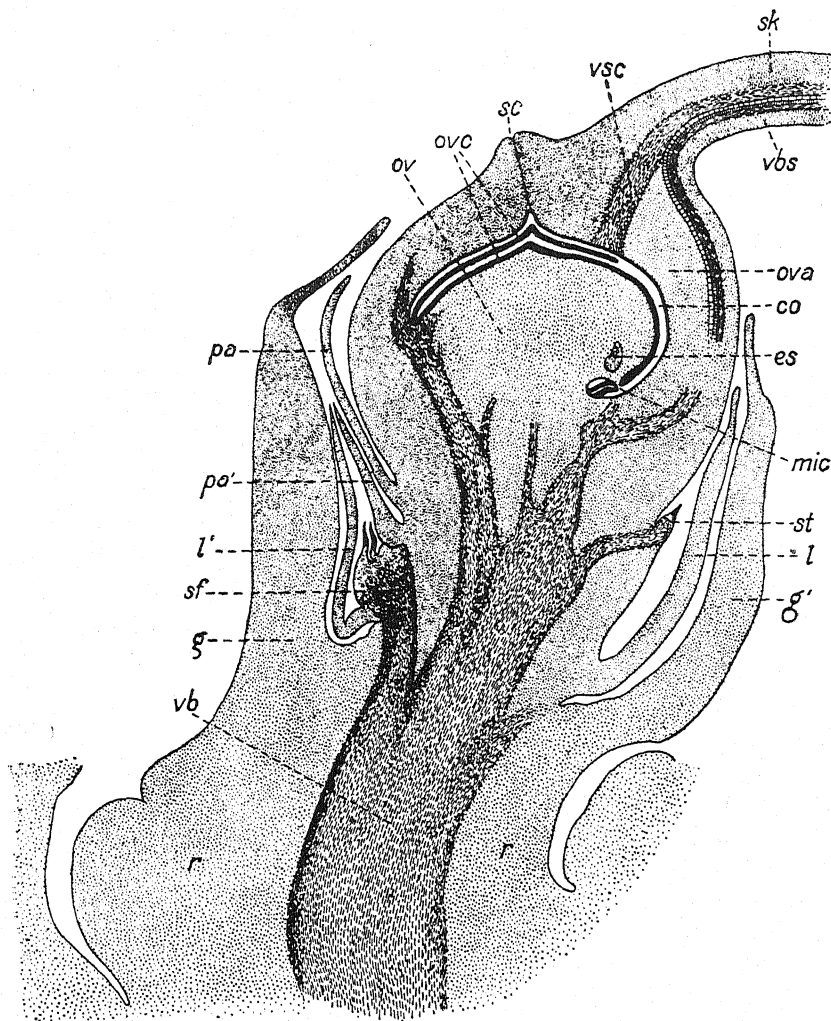


FIG. 156.—Longitudinal section of the pistillate spikelet at the time of pollination: r, rachilla; g, lower empty glume; g', upper empty glume; l, lemma or flowering glume of the fertile flower; l', lemma or flowering glume of the sterile flower; pa, palea of the fertile flower; pa', palea of the sterile flower; sf, sterile flower; st, rudimentary stamen of the fertile flower; ova, ovary of the pistil; co, cavity of the ovary; sk, silk or style; sc, stylar canal; vbs, one of the fibro-vascular bundles of the silk.

Through the sheath cells that surround the bundle, the pollen tube travels down the silk; vsc, sheath-like cells through which the pollen tube travels from the vascular bundle to the cavity of the ovary; vb, fibro-vascular bundles that supply the parts of the spikelet; ov, ovule; ovc, ovule coats; mic, micropyle; es, embryo-sac. X 45. (After Miller.)

*Perianth*.—The two fleshy truncate lodicules probably represent the perianth. They are inserted opposite the lemma and alternate with the stamens. They appear to serve the same function in maize as in wheat.

*Androeceum*.—Three stamens (one dorsal and opposite the palea, the remaining two opposite the lemma) are about equally distributed round the apex. The filaments are at first short, elongating at anthesis. The anthers are bilobed, versatile and may be purple, pink or green in colour according to the genetic constitution. They open by a short slit at the distal end.

*Gynaeceum*.—This is represented in both flowers by a rudiment.

The upper flower of a spikelet matures first; the spikelet is therefore determinate in its development.

**PISTILLATE SPIKELETS**.—The paired pistillate spikelets are arranged in rows along the axis or cob. Both spikelets are sessile and identical.

At the base of the whole spikelet there are 2 glumes. They are shorter than the ovary, broad and fleshy at the base, thin and membranous above and fringed on the edges.

Two flowers are found within the spikelet. The lower flower is reduced to a lemma and palea, both being short, broad and membranous, the former larger than the latter. The lodicules may be present as minute scales. Careful examination also reveals a trace of the missing pistil and the 3 stamens.

The upper flower is pistillate. The lemma is short, broad and membranous and the palea very similar, equal or even larger than the lemma. The lodicules are generally absent and the rudiments of the 3 stamens may sometimes be detected. The bracts as a whole never cover the ovary unless fertilization is prevented; in that case they continue to grow and ultimately completely enclose it. In pod corn, however, they are longer to commence with, and they continue to grow after fertilization until they more than invest the grain.

*Gynaeceum*.—The maize pistil is apparently the product of 3 carpels, two extending to form the silk and the third bearing the ovule (Walker, 1906). Its single basal ovary is somewhat short and dome-shaped, and ends in a fine thread-like structure, the silk. This may reach a length in some varieties of 18 inches—the actual length reached depending in part on the time of fertilization. It is solid, flattened and grooved on either side, green, red, salmon, brown or purple in colour; its tip divides at the apex into two unequal lobes; short multicellular hairs clothe the surface for some distance from the tips; two fibro-vascular bundles run throughout its length. The nature of the silk is under dispute. Earlier authors regard it as a style, the cleft apex being considered as the stigmas. Weatherwax interprets it as a compound stigma, the short knob-like protuberance on the top of the ovary being regarded as the style. In the centre of this protuberance is a funnel-shaped depression, leading to what was in the earlier stages a narrow opening communicating with the cavity of the ovary—the so-called stylar canal of Grignard.

The ovary is of variable thickness. It is composed of an outer epidermis, a middle parenchyma of from 8 to 20 cell layers and an inner epidermis similar to the outer.

*Ovule*.—The modified campylotropous ovule is attached to the base of the

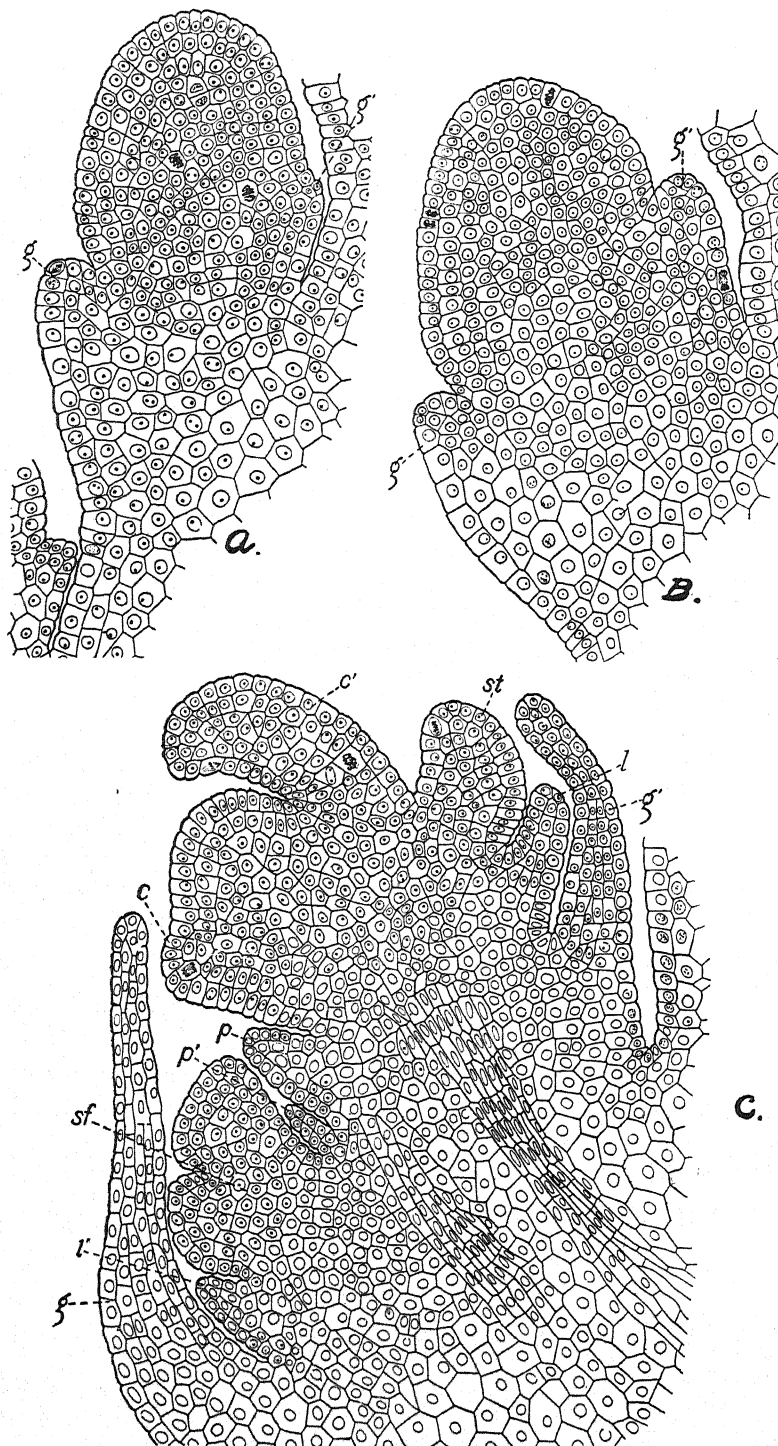


FIG. 157.

ovary chamber by roughly one-third of its circumference. There are two integuments. The outer coat extends to the micropyle on the lower face; about half-way round on the outer. According to Johann, however, the outer integument may be more complete than is generally believed. Below the stylar canal it forms a wedge-shaped projection which passes into the inner depression of the canal. Except at this point, it normally consists of two cell layers. The inner integument—which is free from the outer—invests the whole ovule except at the micropyle. It, too, shows a projection, though less marked, below the stylar canal. It is normally 2 cell-layers thick, except at the projection just mentioned and at the margins of the micropyle.

The mass of the ovule—the nucellus—consists of parenchymatous cells invested by an epidermis. The inverted embryo-sac lies near the base of its inner face. At the time of fertilization it is flask-shaped. The antipodal tissue, a group of 24 to 36 cells, the product by division of the three original antipodal nuclei, lies at the end farthest from the micropyle. At the micropylar end are the 2 lunar-shaped synergidae with dense deeply staining contents and indistinct nuclei. Between the synergidae lies the ovum, a somewhat oval alveolar cell with a large nucleus.

The 2 polar nuclei lie in close contact, embedded in a strand of cytoplasm that stretches from the antipodals to the egg. On either side of this strand is a large vacuole. (Miller, 1919; Weatherwax, 1917, 1919, 1923.)

**DEVELOPMENT OF THE STAMINATE SPIKELET.**—The early stages are somewhat similar to that found in the pistillate spikelet (q.v.). The four sporangia differentiate early. Each consists of a long column of sporogenous tissue surrounded by tapetal layers. This tissue multiplies for a time; its cells then enlarge at the expense of the tapetal, and become the pollen mother cells. The first division (heterotypic) within the mother cells is the reduction division. In this division the number of the chromosomes is halved (Kuwada, 1911). The heterotypic division is immediately followed by the homotypic division, and the 4 cells thus formed round themselves off as the pollen grains. (Reeves, 1928.) The pollen grains so formed are almost spherical. The intine is thin, the exine thick and minutely tuberculate. There is a small germ pore and the contents are dense. Before liberation, the nucleus divides; one of the two then again divides, so that the mature grain contains 3 nuclei—a poorly organized vegetative nucleus and two narrow curved male nuclei or sperms. (Poindexter, 1903; Miller, 1919.)

Beadle (1931) discovered races of maize which exhibit "polymitosis", the

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- A. Longitudinal section of the developing spikelet, showing the primordia of the lower and upper glumes: g, lower glume; g', upper glume. X 300.
  - B. Longitudinal section of the developing spikelet at a little later stage than B. g, lower glume; g', upper glume. X 300.
  - C. Longitudinal section of the developing spikelet, when the initials of all parts are present. g, lower glume; g', upper glume; l, lemma of the fertile flower; l', lemma of the sterile flower; p, the palea of fertile flower; p', palea of sterile flower; sf, primordium of sterile flower; st, stamen of fertile flower; c and c', primordium of carpel of fertile flower; the upper part c' growing more rapidly than the lower. X 300. (After Miller.)

characteristic being inherited as a Mendelian recessive. In such plants, the nuclei of the pollen tetrads pass into a prophase condition almost immediately after the second division. In the early stages the chromosomes are single but at metaphase some are double and are usually scattered over the spindle. At anaphase they are distributed at random to the poles. Division of the chromosomes has not been seen to occur. Further abnormal divisions then take place, resulting in the formation of 32 cells, each with only 1 chromosome. The pollen so formed is completely sterile. A more or less similar condition is found in the embryo-sac, but some 10 per cent. of the embryo-sacs are functional and haploid.

**DEVELOPMENT OF THE PISTILLATE SPIKELET.**—On the margins of the young cob, numerous projections develop. Each is the primordium of a pair of spikelets, for soon each rudiment divides equally, and from each half a spikelet forms. Following out the development of one of these, we find that the lower glume appears first, followed a little later by the upper glume. The primordia of the 2 lemmas follow, and almost at the same time the rudiments of the sterile flower and the stamens of the fertile. The palea of the fertile follows but that of the sterile does not form until later.

No further development of the stamens takes place, but shortly after the ovary wall of the pistil of the fertile flower appears. It grows unevenly. When the side adjacent to the lemma extends about half-way over the young ovule, the opposite side is only just visible. This rapidly growing side also increases in width towards the tip so that it may become two to three times wider than the base. This region then begins to elongate to form the silk. Meantime, the ovary wall has gradually overgrown the ovule, except for a small opening near the top, the stylar canal. This canal gradually closes and by the time the silk is mature, the edges have met and closed.

Whilst the silk elongates, the ovule—which is at first a dome-like mass of embryonic cells within the growing wall—begins to invert. This inversion is due to the cells adjacent to the palea multiplying and elongating faster than the cells on the opposite side. At the same time, the integuments are rapidly developing, and by the time the ovule is completely inverted, the integuments are complete.

The megaspore mother cell is first visible when the ovule begins to invert. It arises from a sub-epidermal cell and divides by two divisions, the first of which is the reduction division. There result 4 megaspores, only one of which develops into an embryo-sac. This shows the usual series of three divisions resulting in the organization already described. As the embryo-sac develops, the epidermal cells above it and opposite the micropylar opening divide periclinally, forming a 5- to 6-celled beak which projects into the micropylar opening. (Miller, 1919.)

**ABNORMAL SPIKELETS.**—A. OF THE TASSEL.—1. One or more of the spikelets may become hermaphrodite, *i.e.*, they have both stamens and pistil.

2. One or more may become pistillate. In such cases, the stamens disappear. If several are so affected they assume all the characters of the normal pistillate spikelet.

3. A case of "tassel seeds", studied by Emerson (1920) is comparable to the "silkless" described below. The stamens abort very early, and so permit the development of pistils on inflorescences that would normally be staminate only. Both "tassel seeds" and "silkless" appear to be genetic in origin.

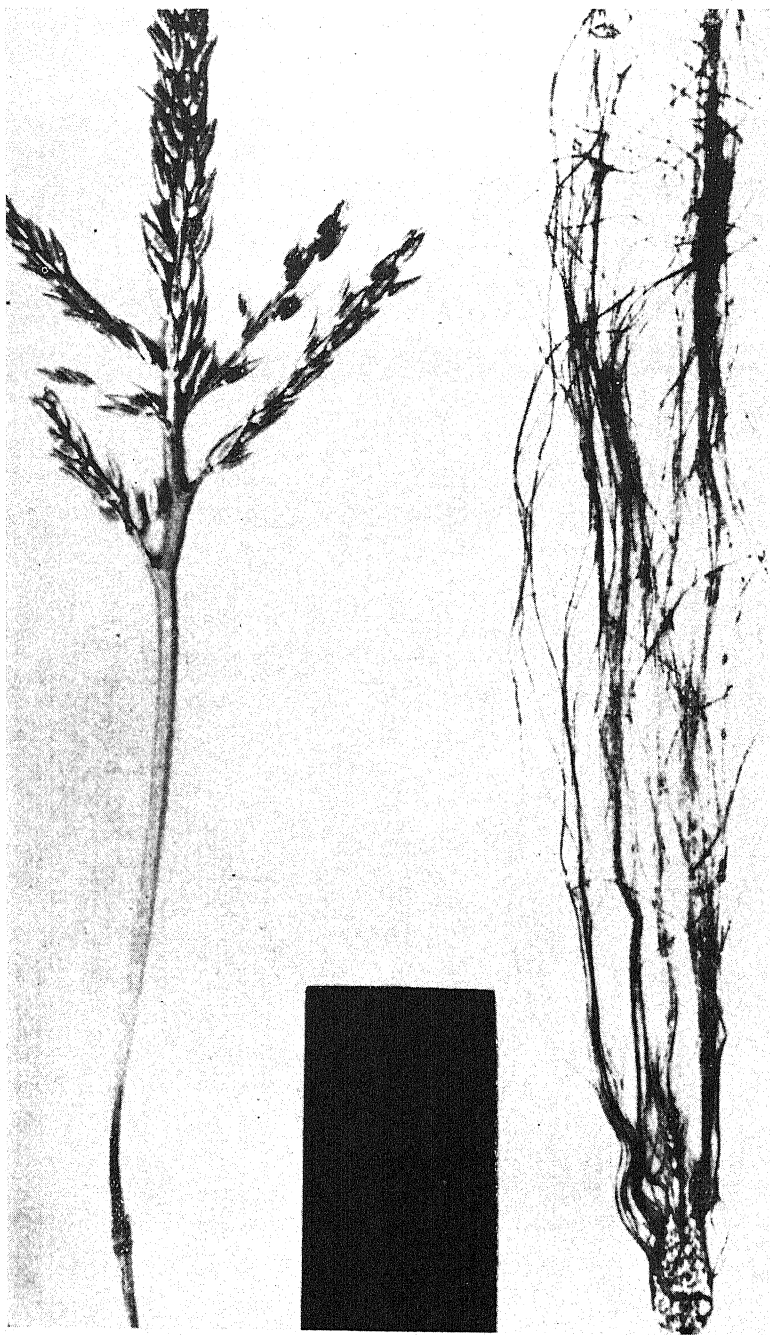


FIG. 158.—Three “tassels” from plants of same plot, developed in decreasing short light condition: (1) normal (male), (2) vestigial (neuter), (3) carpellate (female with neuter tip). (After Schaffner.)



B. OF THE "EAR".—1. The lower flower may be fertile. In such cases each spikelet develops 2 grains. Normally, there is but one, the product of the upper flower. This is the explanation of the fact that the embryo is always on the upper face of the grain. If, however, both flowers are fertile, the position of the embryo on each line of grains will alternate. The number of the grains will also be doubled and, as a consequence, the crowded grains assume the so-called "shoe-peg" shape through mutual pressure on one another.

This phenomenon is regularly met with in several varieties of Sweet Corn. It may occasionally occur in any variety, and leads to irregularity in the rows.

2. The spikelets may be perfect, developing the stamens as well as the pistil. In such cases, the pollen is generally unavailable owing to the fact that the ear is protogynous.

3. One or more (generally more) of the flowers are staminate. The commonest form is the formation of an ear with a staminate tip.

More rarely the staminate flowers occur some distance from the tip. Small groups of such flowers may also occur at any point, producing "ears" with blank spaces.

Forked, branched and fasciated ears may also be found, but their occurrence is abnormal and in most cases due to injury. Normal mutants of such types have, however, been noted.

C. EXPRESSION OF "SEX".—Schaffner (1927), by shortening the length of day, succeeded in obtaining plants whose tassels showed reversal to the pistillate condition.

Maize planted in the greenhouse on November 1st produced individuals whose tassels all showed some female expression. Maize planted the following March and thereafter (*i.e.*, spring and summer plantings) showed little or no reversal. Maize planted before or after November 1st showed a ratio of sex reversal inversely proportional to the length of daylight.

Reversed tassels usually show only slight branching. Further, the internodes below the reversed tassels, may become markedly flexed and the sheaths exhibit husk characteristics.

In a further paper, Schaffner (1930) found that with proper periodicity, seven types of tassels may be obtained: three of pure expression—staminate (male), carpellate (female) and vestigial (neuter); and four sex-mosaics—a staminate-neuter, carpellate-neuter, staminate-carpellate and staminate-carpellate-neuter. In a decreasing photo-period of suitable length, the male expression can be suppressed completely. Experiments with pure lines showed that they react in precisely the same way as commercial varieties.

On the basis of these experiments, Schaffner came to the conclusion that the sex expression exhibited in any one instance is due to the physiological gradient, induced by the environment, and that it is independent of any sex-determining factors.

On the other hand, Richey and Sprague (1932) found that strains of inbred maize tested under identical conditions may differ in their liability to sex reversal. A study of the F<sub>2</sub> generation of these strains and a back-cross of two of the three strains studied, indicated that there was a single major factor difference between

them, with the recessive determining the greater tendency to sex reversal. They were also of the opinion that accessory genes were involved.

That genetic factors do enter into the situation cannot be denied. Up to the present at least 40 genes have been isolated which produce partial or total sterility or modify the expression of either the staminate or the pistillate inflorescence or both.

A typical instance of the interaction of certain of these factors has been studied by Jones (1930, 1931, 1933). A recessive factor, silkless, produces sterility in pistillate flowers, thus rendering the plant a functional male. A second recessive factor, tassel seed, causes the staminate flowers to become pistillate, the plant accordingly being a functional female. When these strains are crossed the F<sub>1</sub> plants are normal monoecious hermaphrodites.

In the F<sub>2</sub>, the double recessives are pistillate. Such a plant crossed with silkless gives all silkless (o) offspring; interbred with themselves, all pistillate. Dioecious strains of maize are thus differentiated.

It is obvious that the inherited constitution as regards the expression is complex, and at present largely unknown.

Further, the expression of any particular constitution is influenced by the environment in which the organism is functioning. The one is inseparable from the other. There is no such thing as an environmental "vacuum".

**ORIGIN OF THE PISTILLATE INFLORESCENCE.**—As we have seen, the pistillate inflorescence is a spike, on whose thickened axis the paired but sessile spikelets are arranged in several longitudinal rows.

The alicoles are therefore polystichous, or many ranked in arrangement. On the other hand, the staminate inflorescence is a panicle, whose central axis is continuous with the main stem. This central axis carries lateral branches which are spirally arranged or polystichous. At the same time, the alicoles of the main axis are polystichous whilst those of the lateral branches are distichous.

In spite of apparent diversity there is little doubt that the alicoles of both types of inflorescence are homologous. "Consequently," as Weatherwax has put it, "the real problem is reduced to an explanation of polystichism in the arrangement of parts round the central axis of the inflorescence."

All the hypotheses advanced have one feature in common—the assumption that the ear has evolved from a panicle resembling the existing staminate inflorescence. On this basis, there are at least four possibilities.

1. **FASCIATION.**—Hackel (1889) attributed the origin of the ear to an inherited anomaly of the nature of fasciation. This explanation was developed and extended by Harsberger and others. Thus, the fusion of 2 spikes, each carrying two rows of paired spikelets, would produce an 8-rowed ear; 3 such spikes, a 12-rowed ear; and so on in multiples of 4.

If this conception were true, one would expect to find in the development of the ear, some indication of its compound nature. No such indication has been obtained. Further, the existence of ears whose row numbers are not in multiples of 4 (e.g., 10, 14, etc., rowed ears) would be impossible. Such ears are common.

2. **REDUCTION.**—This hypothesis postulates that the polystichous ear (as well as the polystichous central spike of the staminate inflorescence of most varieties) evolved from the shortening of the branches in the upper part of a diffuse

panicle, each branch being reduced to a single pair of spikelets. The theory is not supported by the structure found in the staminate inflorescence of most normal maize varieties, where there is an abrupt transition between the uppermost branch and the lowermost spikelets of the central axis. In the type *Zea ramosa*, however, the branches become progressively shorter and pass by imperceptible gradations into simple pairs of spikelets. The transition in this type therefore affords the main evidence in support of the idea.

3. DERIVATION FROM CENTRAL AXIS.—This postulate derives the ear from the polystichous central axis of the staminate inflorescence. It is based mainly on the occasional development of pistillate flowers from staminate ones and the consequent development of more or less ear-like structures within the tassel. The hypothesis does not explain how the central axis became polystichous, but it has the merit of simplicity.

4. TWISTING OF THE AXIS.—Collins (1919), basing his evidence on the structure of hybrids between maize and teosinté, has shown how a maize ear could be produced by the twisting of a 2-rowed pistillate spike accompanied by a shortening of the axis which would produce a "yoking" of adjacent pairs of spikelets. The hypothesis has much to recommend it.

Summarizing the position, it is fairly obvious that no explanation up to the present can be regarded as conclusive. More detailed studies of the inflorescences of maize and its allies; of the effect of environment upon inflorescence structure; and of the comparative structure of the inflorescences of maize hybrids, must be obtained before a satisfactory solution of the problem is possible.

FLOWER OPENING AND POLLINATION.—I. TASSEL.—The first flowers to open are those of the older spikelets near the top of the central axis. Thereafter, blooming spreads upwards and more rapidly downwards. This is followed by anthesis near the tips of the upper branches, proceeding upwards and downwards. As the upper flower of each spikelet opens some time before the lower, a second period of anthesis begins to pass down. This second period begins before the first flowers of the lowest spikelets have begun to open. Further, the pollen from each anther is not immediately discharged, but, owing to the smallness of the pore, requires several hours to accomplish. Under favourable conditions, discharge commences at sunrise and is more or less complete by noon. It follows that a tassel will continue to produce pollen for several days—2 to 14 days, depending on the variety, the relative development of the tassel and the weather conditions. Dry bright weather favours the shedding of the pollen; cold weather delays it.

The pollen grains are nearly spherical, and the surfaces finely tuberculate. They tend to vary in size—pollen from central spikelets is larger than pollen from lateral ones. After shedding, the pollen retains its vitality for about 24 hours. Kempton (1927) noted a change of Mendelian ratio apparently due to the age of the pollen.

The amount produced is enormous. A single anther produces about 2,500 grains; a single spikelet about 15,000; a tassel from 20 to 50 million. According to Lazenby (1898), there are approximately 45,000 grains in dent maize for each ovule.

Insects frequently visit the flowers of maize, but as agents of pollination they are almost negligible. Wind and gravity are the chief distributing agents. From

the elevated tassel, the pollen showers down on a calm day over an area with a radius of some 3 to 4 feet. In a high wind, the pollen may be carried several hundreds of feet.

2. EAR.—The oldest spikelets on the ear are those at the base; the youngest at the apex. The silks of these older spikelets begin to elongate long before the silks of the upper. The difference may be as much as 7 days. But before the silks from the lower flowers escape from the covering husks they have to traverse a much greater distance than have the silks from the upper flowers. This handicap reduces the difference in the time of the appearance of the silks, the ultimate difference being from 2 to 5 days. A silk is receptive whenever it emerges. It remains receptive for some 14 days, and during that period it may continue to elongate until pollinated. As the silks do not emerge simultaneously, but in succession over a period of from 2 to 5 days, it follows that the pollination of every silk on an ear cannot be completed in less than the same period. (Kellerman and Swingle, 1889.) Since the shedding of the pollen during that period may be checked by unfavourable conditions, the actual period of pollination may be spread over a considerable number of days.

HOMOGAMY AND DICHOGAMY.—If the pollen matures at the same time as the stigmas, the flowers are termed homogamous. Such flowers occur in maize, but they are not common. In the great majority of maize varieties, the inflorescences are dichogamous—the pollen and stigmas mature at different times. In such cases there are two possibilities. Either the pollen matures first—the protandrous condition—or the stigmas—the protogynous condition. Protandry has been found to be almost universal in maize, but it is generally not complete. There is usually an overlap of a variable period. In a few varieties, protogyny is constant.

Since homogamy is rare, cross-pollination and therefore cross-fertilization is the rule. Self-pollination, however, does occur. (Hayes, 1918.) This is due to the fact that the protandry—and less rarely the protogyny—is incomplete. Consequently, a limited amount of inbreeding may regularly take place. Weatherwax (1923) states that when plants are grown in hills of 3 to 4 plants, self-pollination of from 5 to 10 per cent. of the grains may take place.

GERMINATION OF THE POLLEN AND GROWTH OF THE TUBE.—Maize pollen may be germinated in various nutrient media. On the silks, the grains are caught on the viscous stigmatic hairs. Germination follows very rapidly. The tube emerges through the germ pore, and may enter the body of the hair and so reach the tissue of the style; or it may grow along the outside of the hair and then penetrate the style directly. Occasionally, a grain may lodge and germinate on the style.

Once within the silk, the tube pushes its way downwards through the sheath-cells of the bundle. The older portion of the tube dies away behind whilst the apex is enlarged. The growing region is apparently nourished by the sheath-cells.

The tube enters the cavity of the ovary via the sheath-cells. Once within the cavity, it twists along the coats until it reaches the micropyle. The rate of growth is rapid. Fertilization follows pollination in from 24 to 36 hours. (Miller, 1919.)

*Abnormal cases of pollen germination.*—In certain strains of maize there is evidence that the behaviour of the pollen is influenced by the physiological constitution. Thus the pollen of the waxy race of maize (*wx wx*) has been shown by

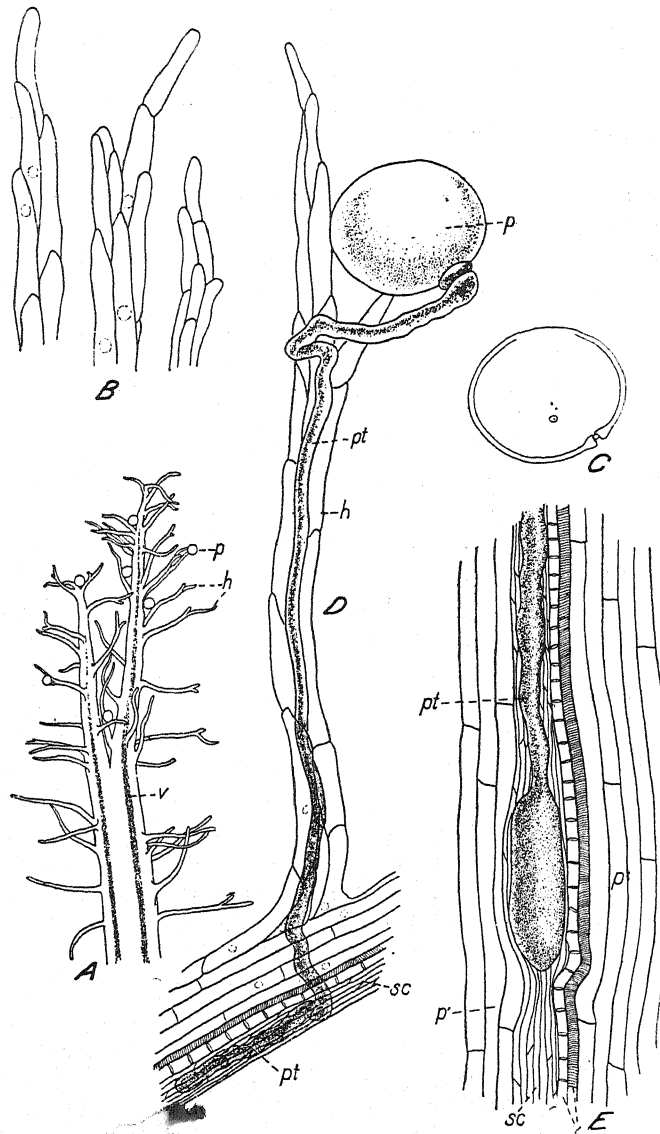


FIG. 159.—Pistillate Spikelet and Fertilization in *Zea mays* L.

- A. End of a silk : p, pollen grains ; v, fibro-vascular bundles ; h, hairs. X 35.
- B. Tips of the hairs of the silk. It is on these hairs that most of the pollen grains lodge. X 250.
- C. Section of a pollen grain showing the germ pore and the relative size of the vegetative and sperm nuclei. X 250.
- D. Single hair of the silk, showing the general manner in which the pollen tube penetrates the sheath cells of the fibro-vascular bundle of the silk : p, pollen grain ; h, hair ; pt, pollen tube ; sc, sheath cells of the fibro-vascular bundle. X 250.
- E. Longitudinal section of a fibro-vascular bundle of a silk, showing the position of the pollen tube as it grows down the silk : sc, sheath cells ; x, xylem elements ; p, parenchyma cells of the silk ; pt, pollen tube, showing the enlarged tip. X 250. (After Miller.)

Brink and McGillvary (1924) and by Demerec (1924 a) to give a red reaction with iodine, whilst the pollen of non-waxy races gives the normal blue reaction. Later, Brink (1926, 1928, 1929 a) found that, in addition to other physiological differences, the extracts of waxy pollen tubes have less diastatic activity than those of non-waxy.

A heterozygous *Wxwx* plant out of the cross waxy  $\times$  non-waxy produces both types of pollen in the ratio of 1 : 1. If a pure waxy plant (*wxwx*) be pollinated with pollen from an F<sub>1</sub> hybrid (*Wxwx*) the seeds show a ratio of waxy : non-waxy in the proportion of 1 : 1. Similarly, if two heterozygous plants be inter-crossed (*Wxwx*), the progeny will consist of non-waxy : waxy in the ratio of 3 : 1. (See under *Xenia*, page 456.) Several authors, however, have shown that in these experiments there is a deficiency of grains with waxy endosperms.

This has been explained on the basis that the growth of the pollen tubes carrying the factor for waxy differs from that of a tube carrying the factor for non-waxy. Brink and Burnham (1927) showed that when the upper and lower halves of the ear were pollinated by pollen from a heterozygous *Wxwx* plant, the same percentage of waxy endosperm grains was produced. They, therefore, concluded that the two types of pollen have differential growth rates at the beginning, identical growth rates later. The early growth rate was attributed to the hydrolysis of the starch or starch-like carbohydrates of the pollen grain; the later growth to the absorption of sugars from the style. Early growth will, therefore, depend upon the rate of starch hydrolysis which will be slower in the case of the waxy as compared with the non-waxy. There will therefore be an initial lag in the growth of the waxy pollen grains.

On the other hand, Sprague (1933) could find no significant difference in the growth rates between pollen derived from plants with the four possible constitutions, viz., *SuWx*, *Suwx*, *suWx*, *suwx*. The time required, however, for the germination of waxy pollen and the establishment of its pollen tube was consistently greater than that required for non-waxy. This difference appeared to be related directly to the degree of contact established between the pollen grain and the stigmatic hair.

Genetic factors may also influence the number of pollen tubes carrying the waxy factor. In an analysis of the data found by Kempton (1919), Mangelsdorf and Jones (1926) pointed out that certain of the F<sub>1</sub> plants gave, when selfed, the expected ratios of waxy : non-waxy, whilst others gave lower ratios of waxy. Thus, if plants giving the expected ratios were termed *N*, and those giving the lower ratios *L*, the possible combinations were *L*  $\times$  *N*, *L*  $\times$  *L*, *N*  $\times$  *L*, and *N*  $\times$  *N*. In Kempton's results, *L*  $\times$  *N* and *N*  $\times$  *N* gave 25.1 and 25.4 per cent. of waxy grains respectively, whilst *N*  $\times$  *L* and *L*  $\times$  *L* gave 22.9 and 22.6 per cent. respectively. In other words, when the *N* plants were used as the pollen parents, the progeny gave the expected ratios (25 per cent.) but when the *L* parents were used there was a distinct departure from the expected ratio. Mangelsdorf and Jones accordingly concluded that an accessory factor is at times coupled with the waxy factor, which tends to reduce the number of fertilizations effected by the pollen tubes carrying the waxy factor.

Further complications have been noted. Thus, Owens had found that the F<sub>2</sub> generation of the cross Rice pop  $\times$  Sugary gave only 16.25 per cent. of sugary

endosperm instead of 25 per cent. If the homozygous dominant *SuSu* (with corneous endosperm) was crossed with the heterozygous *Susu* the progeny gave a large excess of *SuSu* plants (corneous). On the other hand, there was no marked deviation when the female parent employed was homozygous for sugary endosperm (*susu*). Jones (1924) concluded that this result was apparently due to an interaction between the pollen tubes and the stylar tissue of such a nature that the pollen tubes carrying the dominant *Su* factor secured fertilization more readily than those carrying the recessive *su* factor. The result, however, is only obtained when the sporophyte has in addition the dominant factor present either in the homozygous or the heterozygous condition.

Brink and Burnham (1927) also found the *su* factor for sugariness could exert a differential action on *Wx* and *wx* pollen, producing a marked depression of the waxy : non-waxy ratio. This is found only when the pollen parent is homozygously recessive for sugariness and heterozygous for waxy, *susuWxwx*, but not when it is doubly heterozygous, *i.e.*, *SusuWxwx*. They accordingly were of the opinion that the factors *susu* retard the growth of the pollen tubes carrying the *wx* factor.

Finally, Mangelsdorf and Jones (1926) postulate the presence of a factor *Ga*, which is linked to the factor *de*<sup>1</sup> causing defective seeds, and which increases the rate of pollen tube growth. These factors, *de*<sup>1</sup> and *Ga* are further linked with *Su* (corneous). They thus bring into line both the *Su* and *de*<sup>1</sup> factors and suggest that their unusual behaviour in the recessive condition is in reality due to their linkage with *Ga*.

A peculiar race of "high sugary" has also been studied by Mangelsdorf (1931, 1932). The plants of this stock are heterozygous for the recessive factor sugary and when self-pollinated produce 66 per cent. sugary kernels instead of 25 per cent. When back-crossed on the recessive, approximately 94 per cent. instead of the usual 50 per cent. are sugary. The ability to produce these abnormal ratios is transmitted through only about 15 per cent. of the ovules and 1 per cent. of the functional pollen.

All plants belonging to "high sugary" races produce pollen of different sizes. Half the grains are normal in size; the remainder are distinctly smaller, though otherwise normal. The gene believed to be responsible for the production of "tiny" pollen is located on the third chromosome, to the left of *su*, and exhibits a cross-over value of approximately 6 per cent.

Mangelsdorf assumes that the normal sized grains of the heterozygous high sugary plants carried the gene for sugary; whilst the "tiny" grains all carry the starchy gene, with 6 per cent. of cross-overs in both. Further, the tiny pollen grains would function only rarely in competition with normal grains owing to the handicap of their size. The percentage of starchy grains obtained in back-crosses (6 per cent.) is accordingly due to the 6 per cent. of cross-overs present in the normal grains, and is not due to fertilizations affected by the "tiny" grains.

He attempted to prove this hypothesis by sieving the grains. The two classes of grains so separated were shown to carry different genes. The "tiny" grains produced fertilization when competition with the normal grains was reduced or eliminated, and as a consequence the per cent. of sugary kernels present fell from 94 to 25.9 per cent. (in one case 15.3 and on one ear 8.1 per cent.). The failure

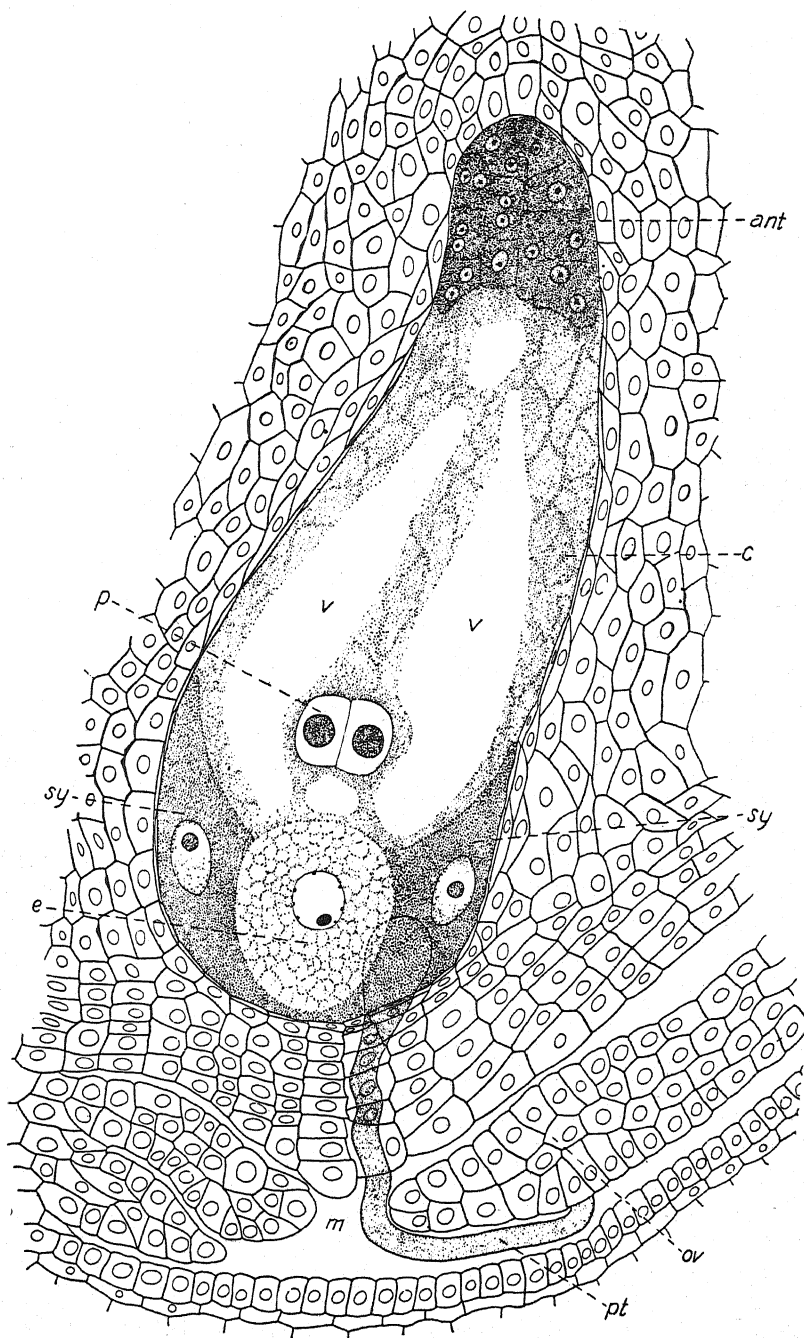


FIG. 160.—Longitudinal section of embryo-sac just previous to fertilization : e, egg ; sy, synergids ; p, polars ; pt, pollen tube ; m, micropyle ; v, vacuoli ; c, cytoplasm ; ov, ovule coat. X 520. (After Miller.)



to obtain 6 per cent. was believed to be due to the fact that some of the smaller grains passing through the finest sieve (0.062 mm.) were genetically normal though tiny.

In the above examples it is clear that the genetic constitution may affect the physiological and morphological constitution of the pollen grains, and as a consequence their reaction to the stylar conditions which are in turn the product of the genetic constitution of the sporophyte.

Recently, a number of so-called semi-sterile forms have been discovered. These forms are now known to be structural hybrids and will be discussed later. (See page 452.)

**FERTILIZATION AND HETERO-FERTILIZATION.**—The pollen tube grows up through the micropyle into the embryo-sac until its much swollen apex almost reaches the polar nuclei. The wall of the tube then dissolves and frees the sperm nuclei, preformed as we have seen, in the mature pollen. One sperm fuses with the egg nucleus; the second fuses with the two polar nuclei, the resulting triple fusion nucleus being the parent of the endosperm nuclei. As a consequence, the expression of this endosperm will be influenced by the genetic nature of the nuclei concerned. (See Xenia.)

The interval elapsing between the entry of the tube into the ovary cavity and the act of fertilization varies from 2 to 4 hours.

Sprague (1929, 1932) has described cases of what he terms "hetero-fertilization". In certain races of maize, the scutellum may be red or purple, due to the interaction of a large number of factors. The interaction of the members of this system may produce homozygous coloured scutellum strains of four different genotypes. Normally, kernels with white aleurone never have coloured scutellums. A few kernels, however, were found with colourless aleurone and coloured scutellum. On sowing the plants from these seeds, segregation for both scutellum and aleurone colour took place. Embryo and endosperm must have been of different phenotypes.

Genetic tests indicated that this difference must have been due to the fusion of the egg and of the polar nuclei with sperms of unlike genotypes. By using mixed pollen, it was further shown that more than one pollen grain may participate in the fertilization process, thus introducing (into the embryo-sac) genotypically unlike nuclei.

Sprague also points out that non-disjunction could produce a similar result but only to a minor extent. Such hetero-fertilizations may occur with a frequency of 1 in 80 in normal cultures and 1 in 4 in high hetero-fertilization stocks.

**DEVELOPMENT OF THE GRAIN.**—A. **EMBRYO.**—When the endosperm nucleus has given rise to some 20 or 30 nuclei, the oospore divides transversely into two unequal cells. The lower and the larger develops into the suspensor, a temporary structure whose function it is to keep the embryo in contact with the food store. This cell divides until it is several cell-layers thick and lengthens so as to keep the embryo in close contact with the endosperm. The pressure is such that it may become twisted. The lower and smaller becomes the embryo. Growth is at first symmetrical. Soon a lateral lobe forms, the initial of the scutellum. Next, the primordium of the coleoptile appears at the morphological apex as an open ring of tissue whose edges ultimately unite. Within the coleoptile

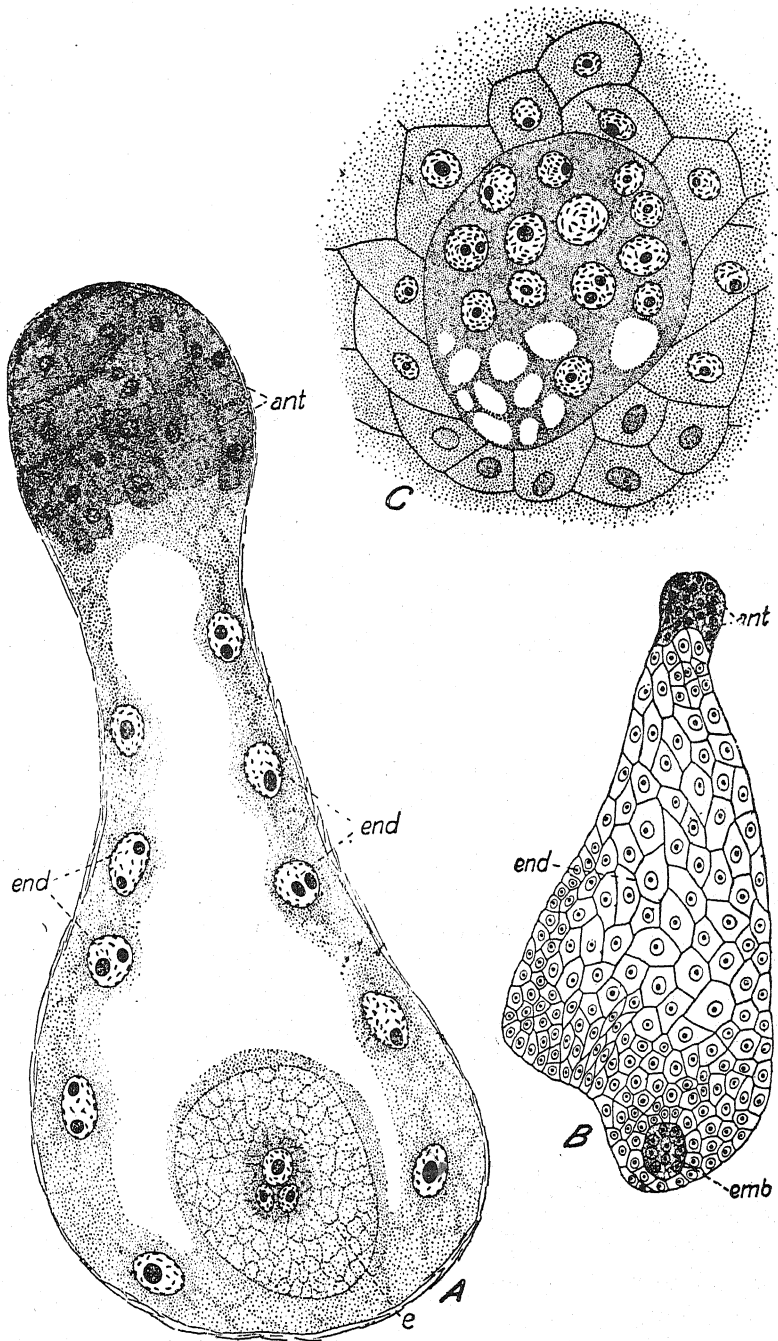


FIG. 161.

- A. Longitudinal section of the embryo-sac 12 hours after fertilization : end, endosperm nuclei ; e, egg in which one of the daughter nuclei has already divided ; ant, antipodals. X 520.
- B. Longitudinal section of the embryo-sac 36 hours after fertilization ; end, endosperm ; emb, embryo ; ant, antipodal tissue. X 110.
- C. Longitudinal section of the young embryo at the stage shown in B. X 800. (After Miller.)

there develop in succession the initials of several foliage leaves, with one or more axillary buds. During the whole of this period the scutellum is rapidly increasing.

The primary root commences as a group of 2 to 3 meristematic cells near the lower end of the main axis between plumule and suspensor. By unequal growth the basal ground tissue is split away from the upper to form the root sheath or coleorhiza. Three lateral rootlets form later; a pair just above the insertion of the scutellum, right and left of a plane passing through the median axis; and a third on the outer face of the embryo at a point corresponding in position to the epiblast rootlet of the wheat.

Opposite the cotyledon and below the rudiment of the third rootlet there may be noticed a region of embryonic tissue. This is regarded as the latent initial of the epiblast of the wheat embryo. As the main axis of the embryo develops, the margins of the scutellum grow round it, until finally only the tip of the plumule is visible from the front. (Miller, 1919; Weatherwax, 1923.)

**B. ENDOSPERM.**—The triple fusion or endosperm nucleus divides immediately and in a comparatively short period up to 50 free nuclei lining the periphery of the embryo-sac are produced. Cell walls then begin to form along the margins, and by centripetal growth from this marginal layer, the whole of the now enlarged embryo-sac is obliterated. The antipodal cells remain intact and may even multiply but they are in the end crushed out by the growing endosperm. (Weatherwax, 1926.)

Impregnation of the endosperm with starch reserves begins in the upper cells, and proceeds downwards and outwards. The protein seems to be deposited from without inwards. The physical differences found in the mature grain are due to the nature and relative amounts of the materials deposited. The main reserves are carbohydrates (in the form of starch) and proteins.

When the endosperm is nearly mature, a series of periclinal divisions in the outermost cells develop the aleurone, a single layer of cubical cells on the surface. Gordon (1922) considers that the aleurone may be regarded as a resting cambium which is responsible for most of the cell divisions which follow the nuclear stage. As the grain enlarges the nucellus disorganizes and is absorbed totally by the endosperm. The epidermis, however, is said by True (1893) to persist as a thin structureless transparent layer immediately beyond the aleurone.

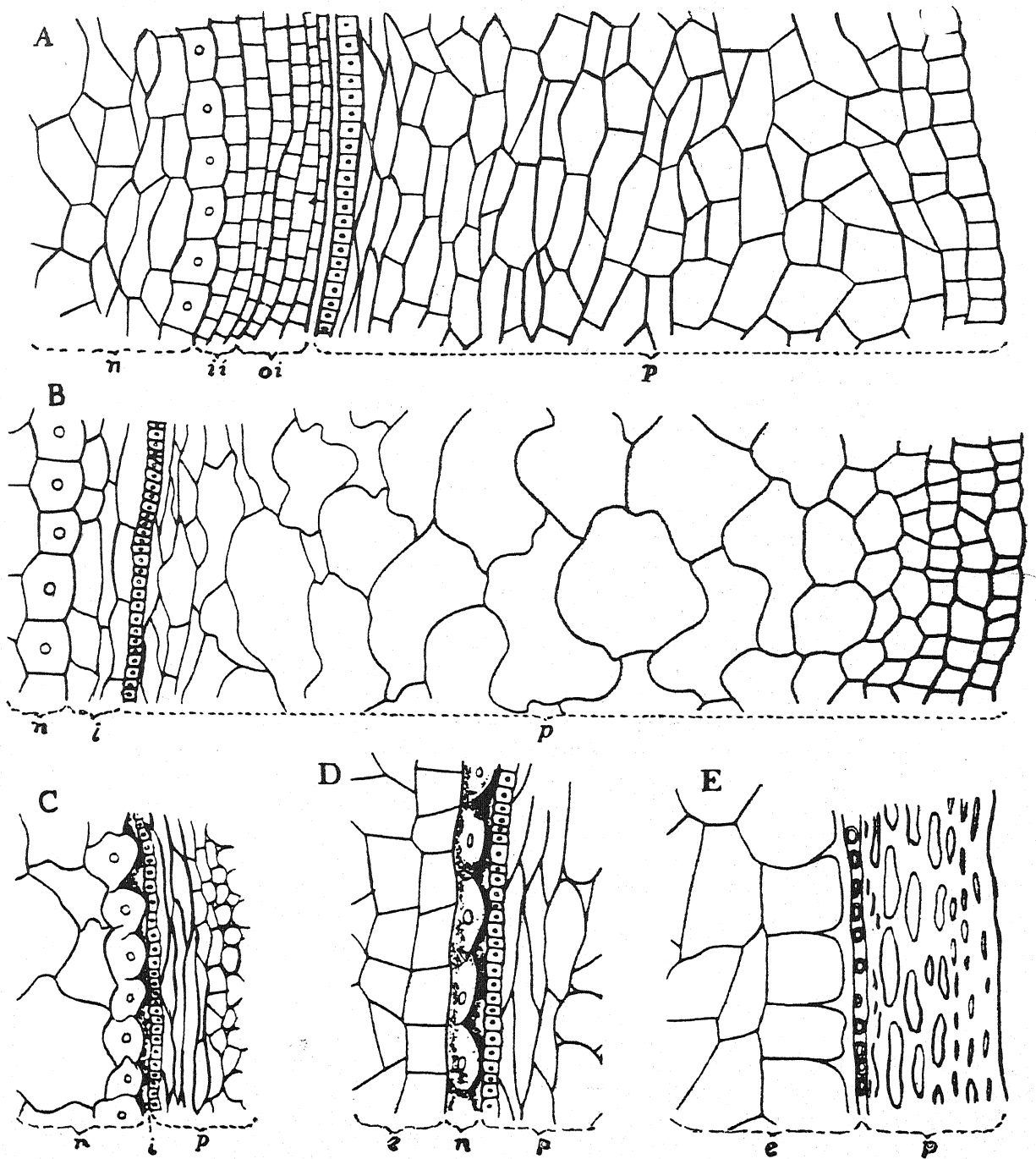
Weatherwax (1930) has discussed the problem of the nutrition of the endosperm and the embryo. The embryo in its early stages is completely surrounded by endosperm except where the suspensor passes to the outside.

FIG. 162.—Cross-sections of parts of kernels, showing development of pericarp and its relation to underlying tissues.

A. At fertilization. B, Early stage of embryo and endosperm development. C, Later stage. D, Still later stage, endosperm formation nearly completed. E, At maturity. *n*, Nucellus; *ii*, inner integument; *oi*, outer integument; *p*, pericarp, or ovary wall; *i*, integuments; *e*, endosperm.

No indication of the development of a suberized semipermeable membrane on the inner wall of the inner integument is here indicated, and there is no trace of the nucellus left.

Compare with this figure, Figures 164, 165 and 166. (After Randolph.)



At maturity, the endosperm appears to be wholly on the scutellar side. Nevertheless, the aleurone at least persists on the outer surface of the embryo. The endosperm cells in contact with the scutellum show disorganization, but in the early stages, very little food could be obtained directly from this source. Possibly the cells of the endosperm next the embryo serve a vascular function transferring food material to the embryo.

Weatherwax also points out that the destruction of the nucellar tissue alone would not be sufficient to feed the endosperm. At the base of the endosperm, however, the cells are relatively small, usually elongated and angular in shape. They appear to be capable of division, and are close to the vascular supply of the ovule. Weatherwax concludes that this specialized region has a placental function.

C. GRAIN COATS.—The grain coat, as in wheat, is of double origin—an outer pericarp, and an inner testa.

1. *Origin of the testa* (seed coat proper).—As the grain forms, both integuments disappear, more or less simultaneously, according to Johann (1936). At maturity, all that remains is a single, very thin suberized semi-permeable membrane, which is laid down along the inner wall of the inner integument in close contact with the nucellar epidermis. (Johann, l.c.)

2. *Origin of the pericarp* (fruit wall).—The ovary wall at fertilization is from 8 to 20 cells thick with an outer and inner epidermis.

The outer epidermis enlarges, its walls thicken, become pitted and a cuticle develops. Several layers of cells below this also become enlarged, and their walls thicken. The chlorophyll layer (the innermost layer of the middle parenchyma) loses its chlorophyll. Its cells branch and anastomose to form a loose parenchyma with large inter-cellular spaces. The inner epidermis forms a layer of tube cells similar to those of wheat.\*

MATURE GRAIN.—As in wheat and all grasses, the grain is a caryopsis, an indehiscent fruit with a thin pericarp enclosing a single seed, whose testa if present is united to the pericarp. When absent, as seems to be the general condition, the endosperm is in contact with and fused to the pericarp.

The mature grain varies in shape. Further, on any ear the shape varies, due to the fact that the basal grains are subjected to pressure by the husk and by one another, and the upper or tip grains are largely freed from the pressure of the other grains.

The surface is smooth except in some soft corns and all the sweet corns. The morphological base is termed the "tip"; it is drawn out into the spongy pedicel. This may readily be broken off, exposing a small pigmented spot opposite the end of the scutellum. The upper end of the grain may be rounded (most flints); or pointed (many sweet corns); or indented (dent corns). The colour is very variable, ranging from white to yellow, red, purple, blue, brown and black. The actual colour is due to the blending of all the layers of colour present.

The embryo is visible externally as a shallow groove on the side of the grain next to the ear tip. This is due to the fact that the grain is normally the product of the upper flower of a spikelet. If the lower flower also produces a grain, the

\* The development of the caryopsis has recently been re-investigated by Longley (Developmental morphology of the Caryopsis in Maize, J. Agr. Res. 53: 881-916. 1936).

embryo faces downwards, a phenomenon which may occur occasionally in any variety, frequently in certain sweet corns (Halstead, 1912).

Lindstrom (1923), Eyster (1924 a and c), and Mangelsdorf (1923, 1926), have reported the presence in cultures of types with "primitive sporophytes", or exhibiting "premature germination". No period of dormancy occurs and the fertilized egg develops continuously.

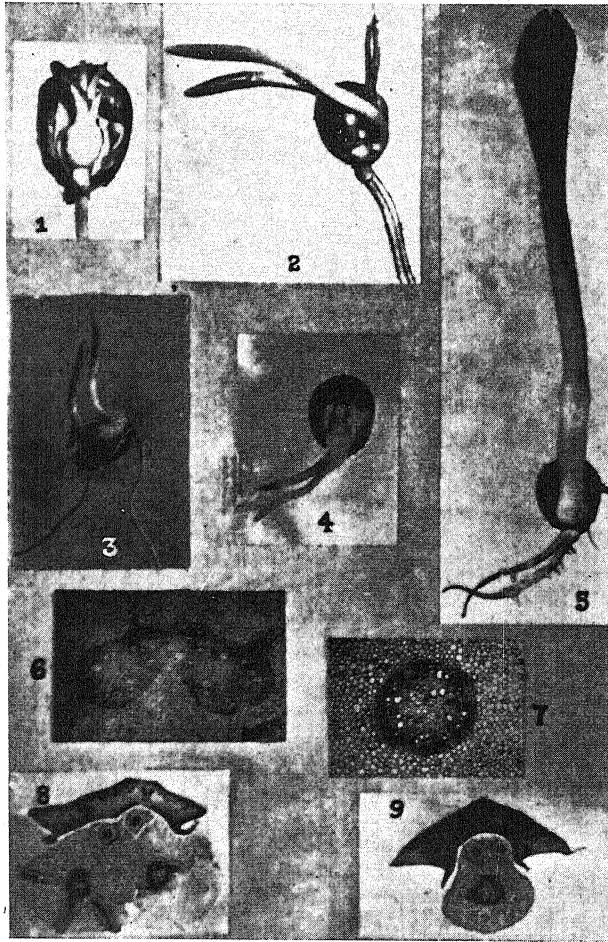


FIG. 163.—Multiple embryos.

1. Normal kernel germinating.
- 2-3. Germinating kernel with two plumules and two primary roots.
4. Germinating kernel with two primary roots and a single plumule.
5. Same as 4, later stage.
6. Cross-section of mesocotyl showing double vascular system of seedling of Figure 5.
7. Cross-section of normal mesocotyl for comparison with 5.
8. Cross-section of germinated embryo at the point of attachment of the cotyledon, showing two stalks and a single cotyledon.
9. Cross-section of germinated normal embryo for comparison. (After Kiesselbach.)



Mangelsdorf (1926, 1930) in an analysis of these races has demonstrated the presence of fifteen recessive factors,  $ge^1$  to  $ge^{15}$ , representing nine different types of germination. Further, the presence in the homozygous condition of certain of these recessive factors produces varying expressions of albinism. It would also appear that the premature germination exhibited is due to the fact that the factors when present induce the formation of enzymes by the scutellum at a very early stage. The normal rest period is therefore broken.

Eyster (1931 b) adopts a more radical standpoint. He rejects his former term "primitive sporophyte" and also the term "premature germination", and refers to the condition as "vivipary". In viviparous maize, there is "continuous development from the fertilized egg to the mature plant, so that dormancy and germination are not involved." He regards vivipary as a primitive plant character which may be inhibited by the interaction of genetic factors and unfavourable conditions. This temporary inhibition is dormancy, and is characteristic of many plants. In the maize strains studied by him 4 recessive genes were found which inhibit dormancy, viz.,  $Vp^1$ ,  $Vp^2$ ,  $Vp^3$  and  $Vp^4$  showing linkage with chromosomes 2, 8, 3 and 1. All were strongly influenced in their expression by environmental conditions.

Examples of embryos with multiple plumules and primary roots have been observed. This condition—one of false poly-embryony—appears to be rare. Much more common is the presence of 2 embryos in one kernel. This condition is due to fusion of adjacent kernels; examples have been found varying from a mere medial point of union to complete fusion. (Wolfe, 1916; du Petit-Thouars, 1920; Blaringhem, 1920; Sutton, 1923; Kiesselbach, 1926 a and b.)

Four structures may be recognized in the grain.

- I. GRAIN COATS.—A. *The Pericarp*, divisible into four layers.
  - a. *Epidermis*.—The cells are elongated, and flattened with thick, pitted walls. A well-developed cuticle covers the outer surface.
  - b. *Mesocarp*.—A series of six or more layers of cells succeeds the epidermis. The outer layers are similar to the epidermal layer, but the walls are thicker. The inner layers are broader, flatter and possess thinner walls. They grade into the next layer.
  - c. *Spongy parenchyma*.—This replaces the cross cells of the wheat. It is the product of the innermost layer of the parenchyma of the ovary, and is composed of branching and anastomosing cells with narrow radiating arms and large inter-cellular spaces.
  - d. *Tube cells*.—These, practically identical to those of the wheat, are the product of the inner epidermis.

*Pericarp pigments*.—A water-soluble purple pigment similar to that found in the sheaths, leaves, anthers, etc., may be present. It results in a cherry pericarp colour. In addition, a rather insoluble orange-red or brick-red pigment may occur; it produces a series of colours from red to orange. Variegated and white mosaic pericarp colour have also been demonstrated.

The factors responsible for colour are numerous, and are believed to constitute a series of multiple allelomorphs. Not only do they affect pericarp colour but

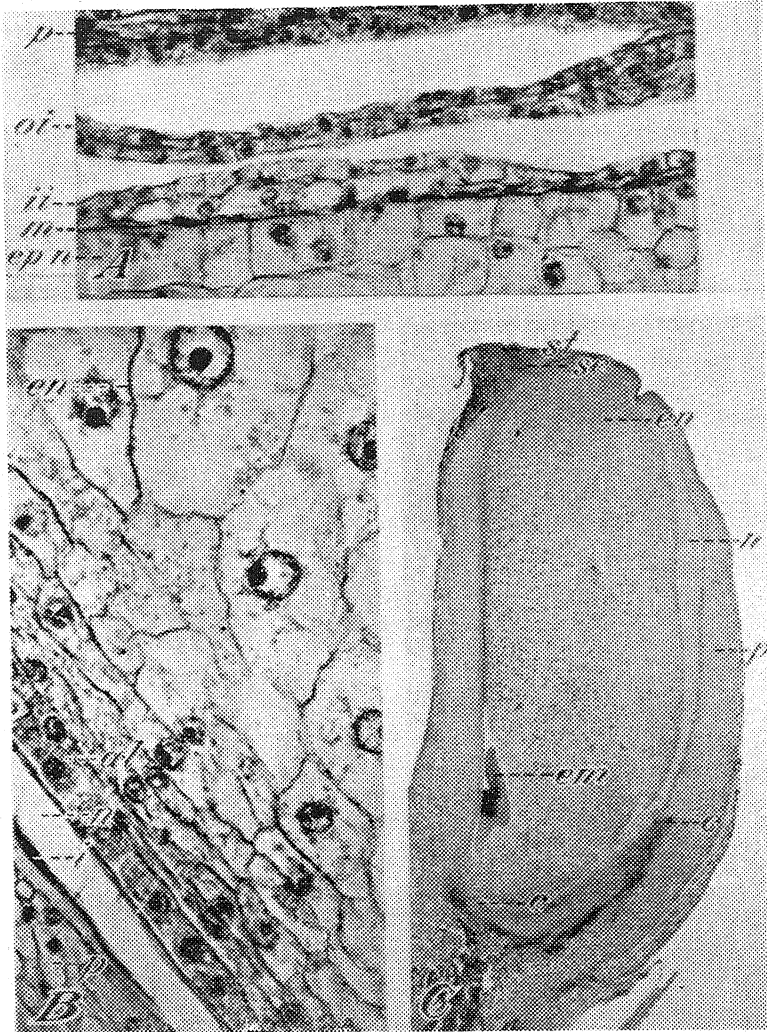


FIG. 164.—Developmental phases of the maize kernel. *A*, Portion of a cross-section of a developing kernel of strain A48, fixed 5 days after pollination, showing degenerative changes in both integuments: *ep. n*, Epidermis of nucellus; *m*, line along which the suberized membranes of the testa will appear; *ii*, inner integument; *oi*, outer integument; *p*, pericarp. Stained with triple stain. X 393. *B*, Detail of *C*. A portion of the endosperm between the embryo and style. At this stage of development, cell division seems to be more active in this region than in any other parts of the endosperm; little starch is to be found in the endosperm. *en*, Endosperm; *al*, aleurone layer (immature); *n*, remains of nucellus; *i*, remnant of the integuments; *p*, pericarp. Stained with triple stain. X 203. *C*, Longitudinal section, showing the relative sizes of the embryo and endosperm in a developing kernel of strain A, open-pollinated, fixed on August 23 at Madison, Wis.: *st*, Remnant of the style; *sc*, stylar canal; *en*, endosperm; *n*, remnant of the nucellus; *p*, pericarp; *em*, embryo; *c*, chalaza; *c-c*, hilar opening through the integument. Stained with triple stain. X 13. (After Johann.)



they also influence plant colour, aleurone colour, silk and anther colour. (East and Hayes, 1911; Emerson, 1918, 1921; Emerson and Anderson, 1923, 1932; Anderson, 1921, 1924; Anderson and Emerson, 1923; Eyster, 1924, 1925; Meyers, 1927; and see page 401 on plant colour.)

B. *The Testa*.—The testa appears as a thin suberized membrane (Johann, 1936). Randolph (1926) found in most cases no testa present. Pericarp and testa together form the "hull," approximately 6 per cent. of the grain.

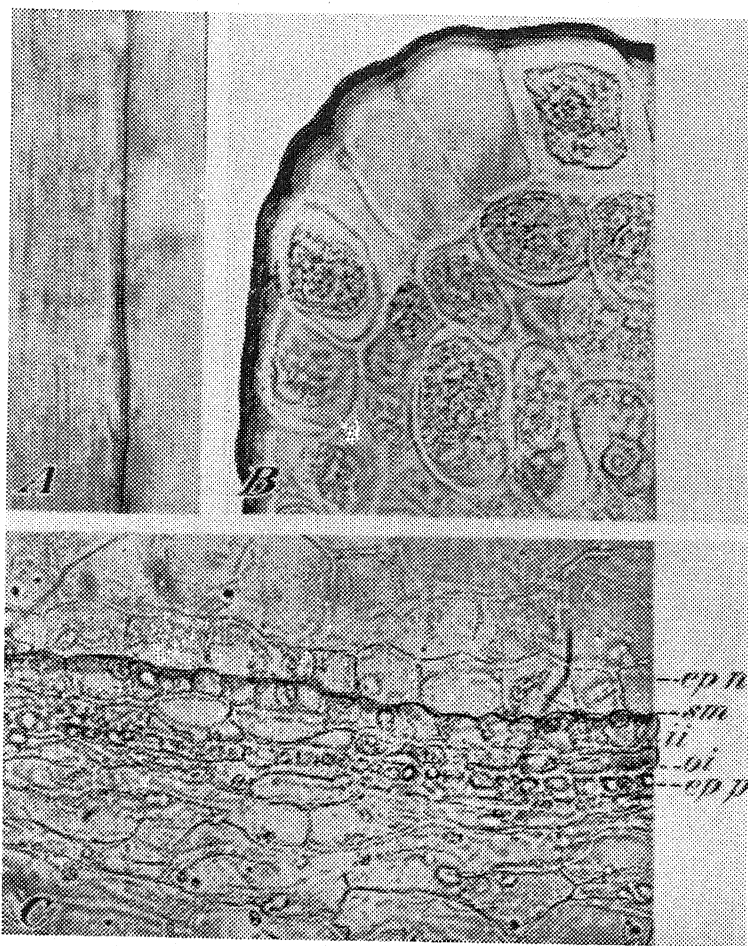


FIG. 165.—The suberized membrane of the testa. *A* and *B*, Sections from a maturing kernel of inbred Lan grown at Bloomington, Ill., showing the relative thickness of the suberized membrane of the testa over the embryo (*A*) and the suberized layer over the tip of the coleoptile (*B*). Stained with Sudan III, mounted in glycerine. X 535. *C*, Portion of a cross-section of a developing kernel of strain A, open-pollinated; fixed on August 19, at which time the silk was beginning to brown. This section is located above the micropyle and shows little of the outer integument. *ep. n*, Epidermis of nucellus; *sm*, suberized membrane; *ii*, inner integument; *oi*, outer integument; *ep. p*, inner epidermis of pericarp. Stained with Sudan III, mounted in glycerine. X 356. (After Johann.)

II. NUCELLUS.—The nucellar epidermis, a thin transparent layer, is very difficult to recognize and in many grains seems to be absent. (Fig. 166.)

III. ENDOSPERM.—a. *Aleurone layer*.—The outermost layer of the endosperm consists of cells which are polygonal when seen from above, cubical when seen from the side. There is little or no starch. It constitutes 8 to 14 per cent. of the grain.

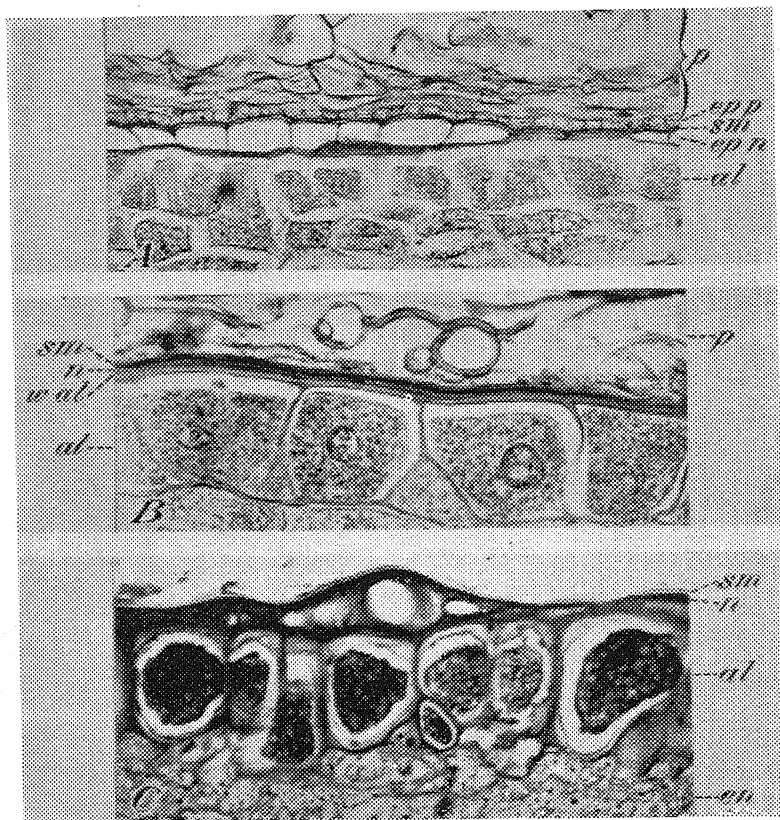


FIG. 166.—Sections showing remnants of the nucellus. *A*, Portion of a cross-section of a developing kernel of strain A, open-pollinated, grown at Madison, Wis., and fixed on September 6: *p*, Pericarp; *ep. p*, inner epidermis of pericarp; *sm*, suberized membrane of testa; *ep. n*, epidermis of nucellus; *al*, aleurone layer. Stained with triple stain. X 335. *B*, Portion of a longitudinal section of the kernel of inbred Lan shown in Figure 165, *A*, *B*. The double nature, in some places, of the broad outer walls of the aleurone cells suggests the presence of remnants of nucellar tissue. *p*, Pericarp; *sm*, suberized membrane of testa; *n*, remnant of nucellar tissue; *w. al*, wall of aleurone cell; *al*, aleurone layer. Stained with Sudan III and gentian violet, mounted in glycerine. X 445. *C*, Portion of a longitudinal section of a dormant, supposedly mature kernel of a Golden Glow strain grown at Madison, Wis., showing what appears to be the remains of the nucellus adhering to the hyaline suberized membrane of the testa: *sm*, Suberized membrane of testa; *n*, nucellar tissue; *al*, aleurone layer; *en*, endosperm. Stained with Delafield's haematoxylin, safranin, and orange G. X 345. (After Johann.)

In certain varieties, the sap of the aleurone contains a pigment (or pigments). This pigment may be either red or blue—red under acid conditions but blue under alkaline. The intensity of the shade of red or blue, and the pattern also vary; in certain hybrids it may even show a mosaic. The normal types are purple, red, variegated or colourless.

b. *Horny and starchy endosperm*.—The cells of maize endosperm are somewhat similar to those of wheat. The physical differences found are in large measure due to the nature and the relative amount of the cell contents. Two main types are distinguishable, hard, corneous or flinty, and soft or starchy. The endosperm of practically all varieties is composed of varying amounts of both. The colour varies from dark yellow, light yellow to white.

All the endosperm cells possess starch granules embedded in a colloidal protoplasmic matrix, containing the protein and certain carbohydrates. In yellow maize and certain other coloured varieties this matrix is associated with a yellow alcohol soluble pigment of doubtful nature. If the matrix is insufficient to fill all the interstices between the starch grains, the endosperm is more or less opaque, soft and "starchy". When the colloidal matrix fills the interstices (in this case, generally smaller), the endosperm is hard, translucent and "corneous". Generally speaking, hardness is a fairly accurate index of the amount of the protein. This test, however, can only be applied to individual caryopses, and to the caryopses of varieties in which the starch grains are uniform in size and shape. The test fails when comparisons are made between varieties whose starch grains are not uniform. Thus, hard flinty varieties with protein content less than that of certain softer varieties are known. In the former, the starch grains are large, angular and closely fitted together; the interspaces are all small and filled by the protein-containing matrix. In the latter, the starch grains are smaller, rounded and closely arranged. The interspaces are large and unfilled—though the total quantity of matrix is greater than in the former instance. As a consequence, the endosperm, in spite of its higher protein content, is relatively opaque and "soft".

The deposition of the reserves begins in the outer cells and progresses centripetally inwards. Hence the physical differences produced by the relative deposition of the reserves is localized in definite areas from the exterior to the interior. There is always a certain amount of opaque floury endosperm in the centre and in contact with the scutellum. The horny endosperm generally covers the whole of the exterior of the endosperm. Its inward extent depends on the variety.

In soft varieties, it is a thin shell covering the main mass of floury endosperm; in flints, it is considerably thicker; in pop corn it may extend inwards until there is only a trace of the floury endosperm in contact with the scutellum left. In all these varieties the hard outer layer effectively prevents any shrinkage of the surface. In the dent corns, the horny layer extends inwards for some distance, but it does not cover the apex. There is here an outer and flinty zone and an inner floury core. The greater shrinkage of this inner core is responsible for the development of the dent. In sweet corns, all cells contain at first a protein carbohydrate colloidal matrix in which starch granules begin to form. These grains do not mature. The race has lost the ability to produce fully developed grains. There is no true horny endosperm and, as a consequence, the whole surface

wrinkles as the grains dry. Nevertheless, though the surface wrinkles the endosperm when thoroughly dry is translucent and flinty—each cell containing small irregularly-shaped starch grains completely embedded in the matrix.

An endosperm of a waxy nature—containing a carbohydrate of a different form from that of the normal starchy type—is known in a race of Chinese origin, and is recessive to the normal. (Collins, 1909 b.)

The “popping” of corn on heating is a property belonging to the endosperm of most varieties. It is best seen in the flinty types, and is at a maximum in the small, hard “pop corns”. It is probably due to the expansion on heating of the moisture in the kernel and, to a limited extent, the constitutional water freed by the partial breaking down of the starch molecule on heating, the pressure being retained for some time by the dense colloidal matrix. This retention causes a sudden ultimate release—the grain as a consequence is ruptured and the endosperm turned inside out. (Wilbert, 1903; Kraemer, 1903; Storer, 1904; Carr and Ripley, 1921.)

Stewart (1923) states that “a moisture content of 13 to 15 per cent. appears to be the most favourable for maximum popping yield.” Willier and Brunson (1927) found about 12 per cent. to be the optimum for greatest expansion. Further, “within a given variety, those ears having kernels with the least soft starch are likely, on the average, to give the largest expansion”; and similarly, “those ears having smaller kernels are likely to give higher expansion than those with larger kernels.”

Jones (1920) and Mangelsdorf (1926) have described grains with defective endosperms. The latter author succeeded in isolating 14 factors ( $de^1$  to  $de^{14}$ ) associated with deficiency, each factor being recessive to the normal and producing varying degrees in the expression of the endosperm. Thus  $de^1$  gives an endosperm which is half the normal size;  $de^{14}$  an endosperm which is only a fraction of the normal; the other factors in the series give intermediate expression. Mangelsdorf also found a further factor, termed  $de_{pi}$ , which is called “plant factor”, influencing the sporophyte in such a way that all the seeds produced by it are abnormal. He further found a factor “brittle”, which is intermediate in its expression of the endosperm character between “sugary” and “shrunk”, and finally showed that the five characters waxy, floury, shrunk, brittle and sugary and the fourteen defective endosperm types caused by  $de^1$  to  $de^{14}$  could be arranged in a series according to the percentage of defect produced (Fig. 167).

At least eighteen dominant factors must therefore be present in maize to produce the normal endosperm expression. Any one of these present in the homozygous recessive condition will result in a reduction in the expression of the endosperm.

Other investigators (Eyster, 1922; Lindstrom, 1923; Demerec, 1923; Garber and Wade, 1924; and Wentz, 1924) have described additional forms of abnormal development.

As regards the endosperm characters as a whole, a number of factors are now known which influence the expression. Thus in addition to the complementary factors *ACR* for colour, *pr* develops red, and *Pr* purple aleurone, *in* acts as an intensifier and *i* as an inhibitor of colour; *Bn* produces brown aleurone, whilst *bl* and *S* result in blotched and spotted aleurone. Further, the expression of the

colour may be influenced by the character of the underlying endosperm. (For references see under "pericarp colour", page 428, and also Fraser, 1924; Kvakan, 1924; Hayes and Brewbaker, 1926; Eyster, 1934; Emerson *et al.*, 1935.)

The Y series is responsible for yellow endosperm, and is independent of the aleurone colour. The nature of the endosperm is also influenced by *fl* (floury), *sc* (scarred), *su* (sugary) and *wx* (waxy). The series influencing the development of the endosperm has already been referred to. These factors are distributed in ascertained linkages over at least 7 of the 10 chromosomes.

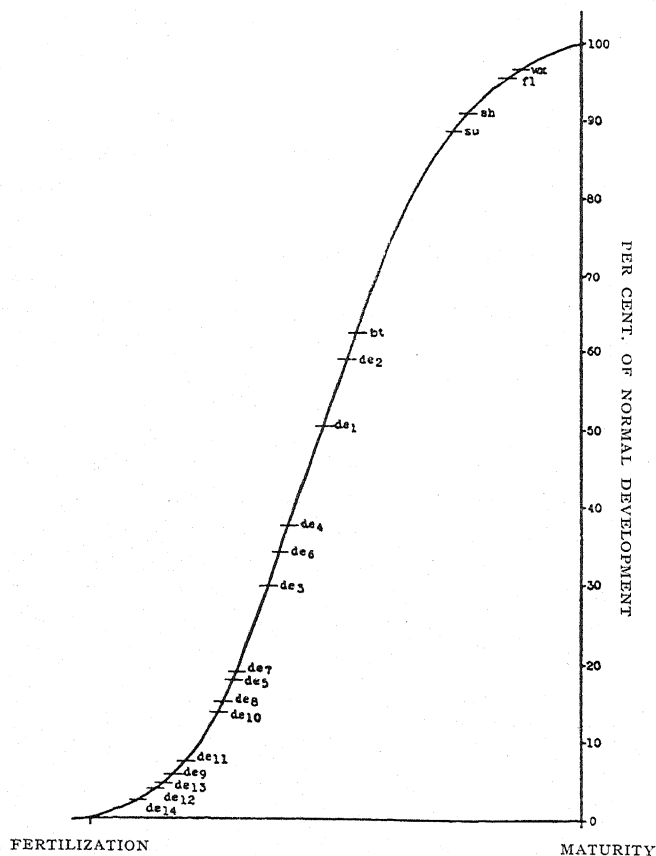


FIG. 167.—Diagram in which the relative development of endosperm characters is represented by points on the growth curve of normal seeds of maize. (After Mangelsdorf.)

Endosperm chimaeras for each of these linkage groups are known. Some are frequent, 9 per 1,000 for *A*; less than 2 per 1,000 for *su*. X-ray treatment after fertilization and irradiation of pollen may increase these deficiencies.

It has been suggested that the deficiencies are due to the loss of a chromosome or a part of a chromosome. If this occurs at the first division a chimaera would result showing the deficiency in about half of the endosperm; if at a later division smaller deficiencies would occur. (Emerson, 1915, 1921.) In natural chimaeras

deficiencies of varying sizes are known. They also occur in treated material. Stadler (1930) found that in both treated and untreated material, deficient areas might revert to the normal, the "recovery" apparently not actually with a higher frequency in treated material. These areas of non-deficient endosperm vary in size, but are usually small.

The facts suggest that "deficiency" may be due in certain instances not to the loss of a chromosome or a part of a chromosome but to some form of "inactivation". There is, however, no evidence for the existence and transmission of genetically inactive chromosomes. Indeed, Randolph (unpublished paper read at the Amer. Assoc. Adv. Sci., 1929) found that deficiency induced by X-ray treatment of the embryo or the pollen, generally involved the loss of a chromosome or a detectable part of a chromosome. Stadler, however, suggests that the chromosome or part of the chromosome may not be lost but ceases to divide. Such a chromosome or part of a chromosome may accordingly be present in a cell or cells without functioning. Should, however, it recommence to divide it would once more become functional and any cells produced therefrom would be non-deficient.

IV. EMBRYO.—The size and the shape of the embryo varies in the different races, and to a less extent the varieties. Its structure is well seen in certain of the large flat dents, and has been studied by a number of investigators. (Rowlee and Doherty, 1898; Sargant and Robertson, 1905; Sargant and Arber, 1915; Weatherwax, 1920; Brunson, 1928; Avery, 1928 and 1930.)

Three structures are obvious, (1) the scutellum, (2) the plumule and (3) the root system.

1. *Scutellum*.—In outline the scutellum is an oval shield. The outer face is slightly concave; the inner face is markedly convex, especially near the base and the middle. Normally, it is white to creamy in colour, but races with coloured scutellums—purple and red—are known. (Sprague, 1932.) On the outer face (best seen when the grain coat has been removed) a faint groove runs up the centre. This groove starts at a point not far from the lower end; it becomes less obvious about the middle, then more obvious in the region of the mesocotyl; and ends finally as a definite ovate opening some distance from the apex. The groove is produced by the margins of the scutellum overarching the main axis, and thus rendering it almost invisible except where the groove widens at the top—there the plumule tip is just visible. (Fig. 168 (1 and 4).)

Immediately above the plumular point the scutellum may project to a slight extent but there is no ventral scale as seen in certain grasses (*e.g.*, wheat and oat). Structurally, the scutellum is largely parenchymatous. The surface in contact with the endosperm, however, is differentiated as an epithelial layer, often with infoldings interpreted by Sargant and Robertson (1905) as epithelial glands. A single procambial strand passes upwards to the apex and branches throughout its length: several smaller procambial strands supply the lower part of the scutellum. At the level of the divergence of the scutellum from the axis, these bundles unite and pass outwards into the stele of the axis. The main bundle of the scutellum as it differentiates is collateral at the base, but tends to become amphivasal towards the apex (Avery, 1930).

In the early stages of development, the scutellum develops rapidly and appears almost as if it were terminal and not lateral in origin (Weatherwax, 1920).



2. *Plumule*.—The plumule is terminal on a short axis, the “mesocotyl”. Sargent and Arber (1915) interpreted this axis as a fusion of the hypocotyl with the stalk of the scutellum; others regard it as the first inter-node (Avery, 1930), or the first and second inter-nodes (McCall, 1934). The growing point at the apex of this axis is protected by a series of overlapping modified or rudimentary leaves. The first of these is the plumule sheath or coleoptile which completely encloses

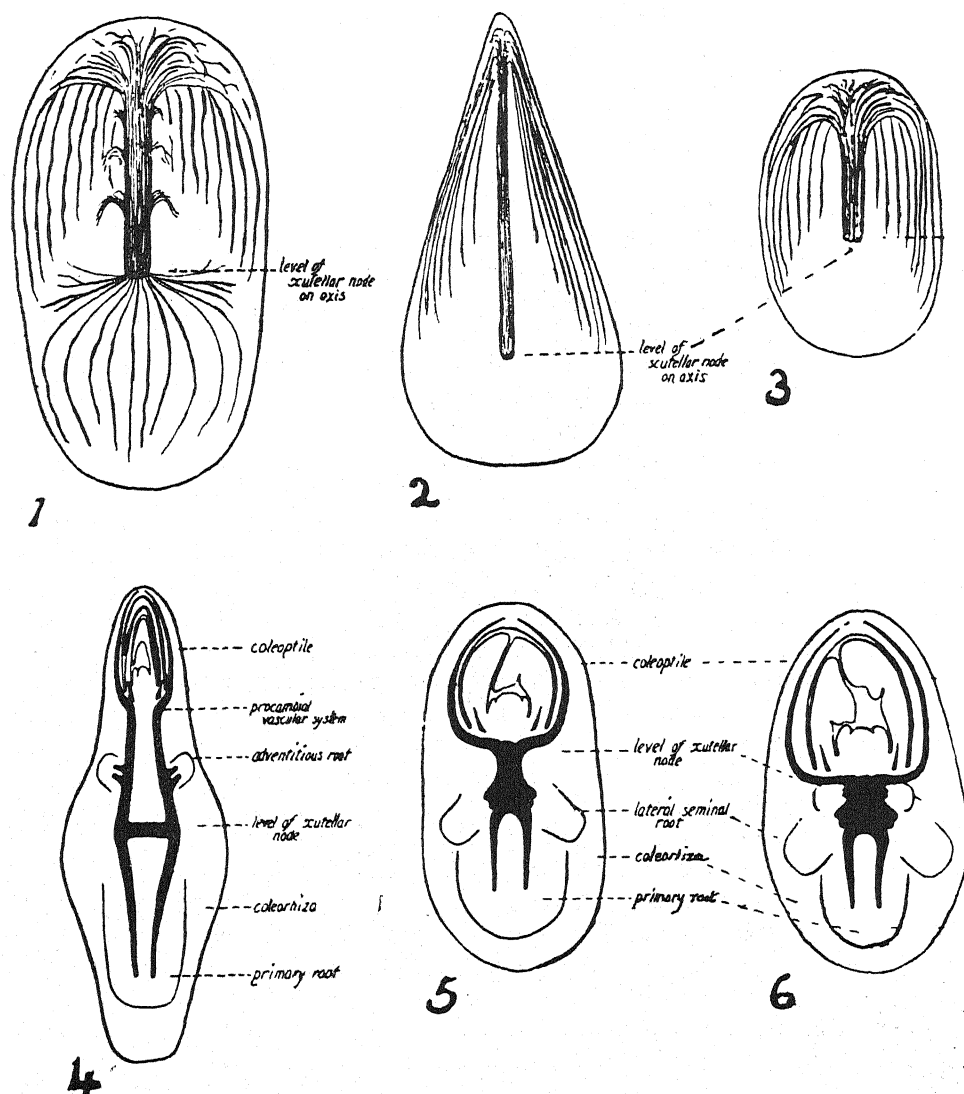


FIG. 168.

- 1-3. Face view diagrams of scutella of *Zea mays*, *Avena sativa*, and *Triticum vulgare* respectively, showing procambial vascular systems.  
 4-6. Face view diagrams of embryonic axes of *Z. mays*, *A. sativa* and *T. vulgare* respectively, showing procambial vascular systems in black. (After Avery.)

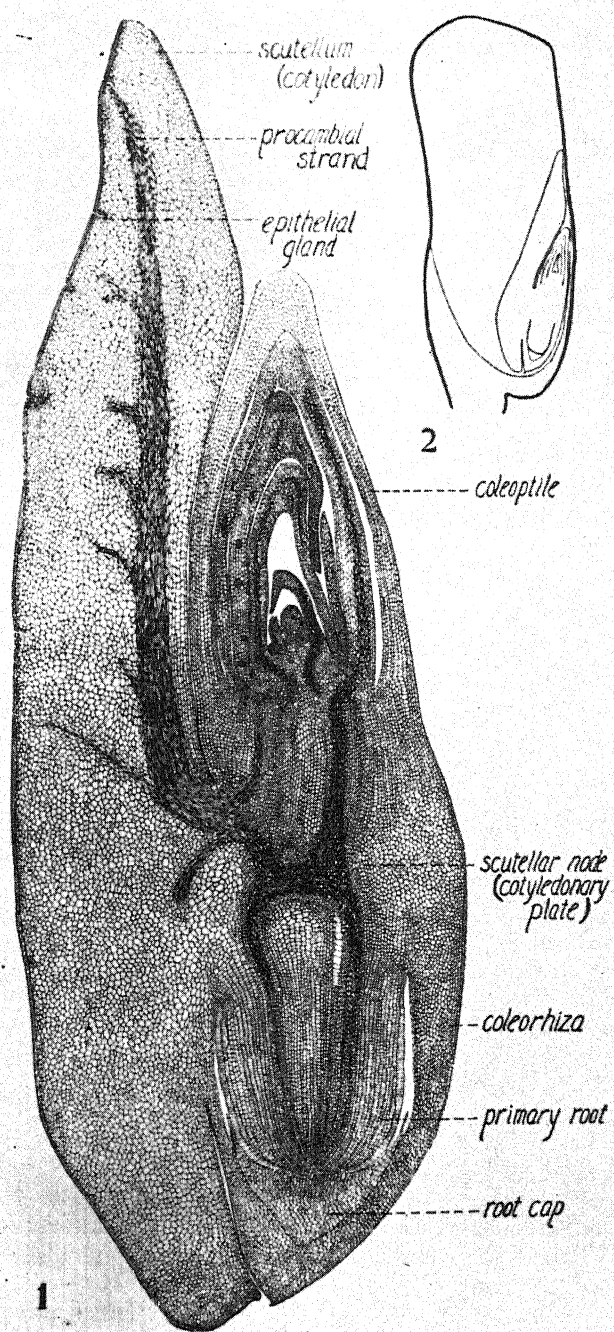


FIG. 169.—*Zea mays* : 1, median longitudinal-side section of embryo ; 2, diagram of median longitudinal-side section of caryopsis, showing location of embryo. (After Avery.)



the remaining parts. This structure has also been interpreted in many ways. Normally it has 2 bundles, but Avery (1928) has found cases of 2 to 5 bundles. Opposite the coleoptile is the first foliage leaf, followed by the second, the third and, more rarely, the fourth. All are convolute.

The structure of the so-called "mesocotyl" is difficult to interpret owing to its shortness. It is, however, transitional from root to stem, and as it elongates is seen to possess both exarch and endarch bundles (Avery, 1930). At the base the secondary seminal roots develop from its pericycle.

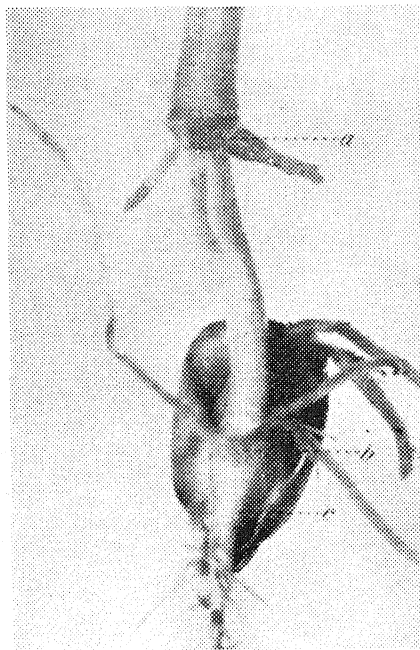


FIG. 170.—Homologies of the seedling of maize according to McCall.

- a. Third node, coleoptile divergence ; crown node.
- b. Second node, scutellum trace divergence.
- c. First node, transition from root to stem.

According to this interpretation, the so-called "mesocotyl" is epicotyl, an elongation of the second inter-node. (After McCall.)

Two bundles on the scutellar side of the epicotyl supply the coleoptile node ; each of these bundles divides and approximately half of each diverges laterally into the coleoptile. The remaining halves continue upwards, giving rise to one or more traces to the true leaf.

Sargent and Arber are of the opinion that the coleoptile bundles appear to be double and have a double origin. They argue that one half of each develops from the cotyledonary bundle, passes up the coleoptile and then turns back on itself to run parallel to and in fusion with the ascending half to pass downwards into the stele. This interpretation, however, is not accepted by others.

3. *Root System*.—The primary shoot is continuous with the main axis at its proximal end. It possesses a definite root cap and the whole is enclosed in the root sheath or coleorhiza. Three additional rootlets are also visible in the embryo. At the base of the mesocotyl a pair develop right and left of the plane cutting the median axis. On the opposite side and just above the position of the missing epiblast, a third root initial is to be found. The departures from the normal already noted may be preformed in the embryo.

4. *Epiblast*.—This structure is absent in the maize; in some sections a zone of meristem may be noticed at the point where the epiblast should appear.

HOMOLOGIES OF THE EMBRYO.—Various explanations as to the homologies of the embryo have been advanced. McCall's (1934) interpretation is as follows.

At the junction of the root and the axis there is, as in wheat and oats, a cross axis vascular plate, which marks the first node. Above this node a zone of tissue on the outer face marks the position of the epiblast (the reduced non-vascular first leaf), which in maize never develops. It is, however, associated with a secondary seminal root. Almost immediately above the first node there is a second node marked by the diverging scutellum trace and the position of the scutellum. The scutellum, therefore, may be interpreted as the second leaf functioning as an absorbing cotyledon. Above the second node 2 secondary seminal roots may be noted. The third node is the coleoptile node, and the inter-node below is the so-called "mesocotyl", in reality epicotyl.

On germination, the second inter-node elongates, raising the third or coleoptile node to a position near to the ground level. (See Figs. 18 (B) and 170.)

Avery, however, considers that the first inter-node has practically no existence, and that the region of elongation is accordingly the first inter-node. Further, he and Boyd do not accept the interpretation of the epiblast as a non-vascular leaf (see under Wheat, page 129 and Oat, page 44).

FOOD CONSTITUENTS OF THE GRAIN.—Hopkins, Smith and East (1903, 1917) have made detailed analyses of the different parts of the grain.

TABLE XXXVIII.

COMPOSITION OF MAIZE GRAINS.

(Extracted from Hopkins *et al.*)

Part.	Per Cent. of whole.	Per Cent. Protein.	Per Cent. Oil.	Per Cent. Ash.	Per Cent. Carbo-hydrates.
Whole grain .. .. .	100.0	10.9	4.33	1.55	83.17
Embryo .. .. .	11.5	19.8	34.8	9.9	35.5
Endosperm .. .. .	88.5	9.7	0.83	0.42	89.0
Embryo as per cent. of grain ..	11.5	2.3	4.0	1.14	4.1

In the endosperm the carbohydrate is mainly starch. There is also a limited amount of sugar. The protein—which consists of zein and globulins—is present as a colloidal matrix within which the starch grains are embedded. In the horny

endosperm, this matrix completely fills the interstices between the grains. In the aleurone layer, proteins and fats are present, but no starch.

The embryo is characterized by the presence of a high percentage of oil. This oil contains over  $1\frac{1}{2}$  per cent. cholesterol, and  $1\frac{1}{2}$  per cent. of lecithin. The protein consists mainly of alkali soluble protein and a small quantity of globulins. The carbohydrate reserve consists of starch and sugar. The starch is present in all the cells of the scutellum (except the epithelium) and also in the plumule, coleoptile and coleorhiza but not in the radicle proper. The sugar consists of sucrose uniformly distributed. There are no reducing sugars. (Chittenden and Osborne, 1891, 1892; Osborne, 1897; Hopkins, 1898; Jodidi, 1925; Larmour, 1927.)

**GERMINATION.**—Sturtevant states that maize germinates in from 10 to 20 days at 43.7 degrees F.; in from 5 to 10 days between 48.6 to 58.5 degrees F. The optimum temperature is given by Sachs as 91 degrees F.; the minimum as 41 degrees F. and the maximum as 114.8 degrees F.

The first change after the grains are placed under conditions suitable for germination is the imbibition of water by all the cells until they become turgid. This water appears to penetrate with equal rapidity over the whole surface of the grain. There is no evidence of a localized semi-permeable membrane as in wheat and barley. A dent grain placed in iodine solution, quickly shows a darkening of the endosperm, first below the dent, and then irregularly over the whole surface. In 24 hours this darkened zone covers the whole grain.

As the cells become turgid, the groove over the embryo widens. The coleorhiza enlarges and in some 20 hours breaks the grain coat and protrudes beyond the surface for about 2 millimetres. The radicle at the same time swells, and bursts the coleorhiza a few hours later. Cell division of its meristem also begins about the time it breaks through.

When the radicle is about 2 cm. long, the cells of the second inter-node commence to elongate and so push the plumule through the grain coats. About the same time, the lateral rootlets begin to develop. The first to appear are the initials which lie right and left of the median plane. Owing to their position, they tend at first to grow upwards between the axis and the scutellum. Later, the third rootlet appears on the face of the seedling above the point of attachment of the scutellum. (For variation in number of rootlets, see page 392.)

About the time of the first elongation of the radicle, the cells of the epithelium begin to swell and elongate. The surface is also increased by the development of fissures. Later, the whole of the scutellum advances into the endosperm by an enlargement of its individual cells.

**UTILIZATION OF THE RESERVES.**—In the early stages of germination the embryo appears to be largely dependent on its own reserves and not upon those of the endosperm. The first detectable change is the appearance of dextrose in the embryo. Whether this is produced from the sucrose, the protein or the starch is uncertain. At any rate the starch of the coleorhiza shows very early evidence of digestion and at the same time the proteins are rendered soluble or undergo partial cleavage. The utilization of the fat is slow. The utilization of the stored food of the endosperm is due to the activity of the epithelial cells of the scutellum. The main secretion is probably diastase—but proteolytic enzymes and it may be

cytase must also form. Reducing sugars—dextrose—appear within 48 hours. The dissolution of the endosperm, however, is much slower than in wheat. (Toole, 1924.)

SEEDLING.—When the coleoptile appears above the ground, the seedling normally possesses 4 seminal roots, 1 primary and 3 lateral. Additional laterals may also form later from the epicotyl. This region (the first or second internode) is also largely responsible for the appearance of the sheath above ground, since

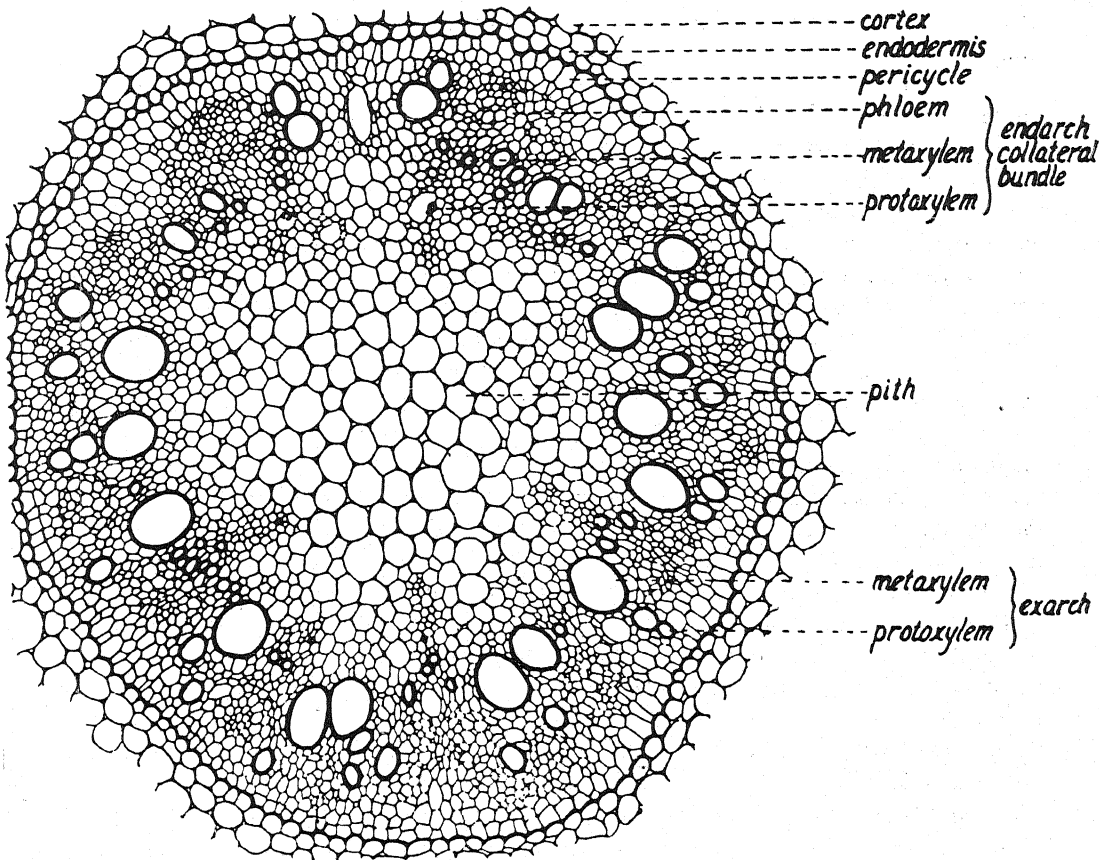


FIG. 171.—Transition from root to stem. (After Avery.)

*Zea mays* : Transverse section of stele in first inter-node of seedling : the second inter-node according to McCall.

it steadily increases in length until the node immediately above it is about an inch or less below ground level. Naturally the length obtained will depend on the depth of planting. If this be over 4 inches, the coleoptile may never reach the surface, the foliage leaves breaking through the split apex below ground. In such instances, the seedling either dies or its subsequent development is markedly retarded. Collins (1914), however, has described certain varieties of maize

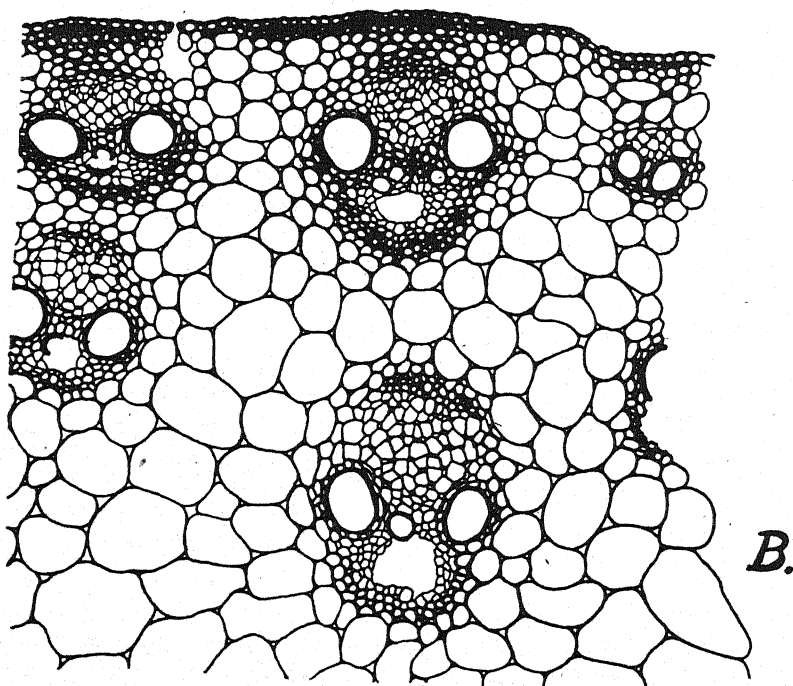
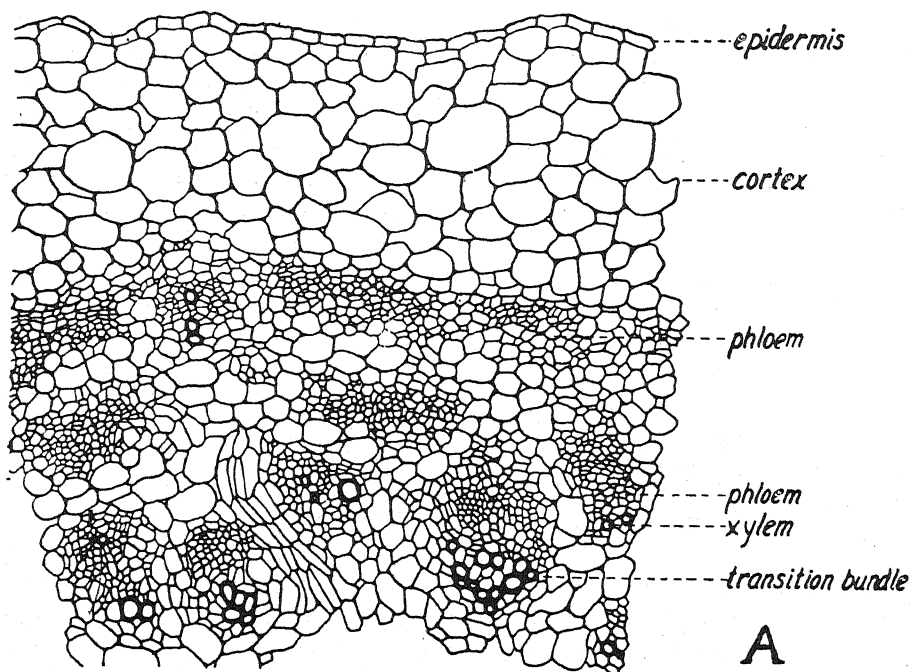


FIG. 172.—Transition bundles at the base of the axis.

- A. At second inter-node (or third) of 3-weeks old plant.  
B. At sixth (or seventh) inter-node of mature plant. (After Avery.)

cultivated by the Indians of the arid south-western regions of the United States, whose epicotyl under deep planting may reach the length of 36 cm. (approximately 18 inches). The coleoptile attains its maximum length, which varies from 3 to 5 cm., in approximately 5 days. Thereafter, chlorophyll develops in the outer layer, especially in the neighbourhood of the vascular bundles, which become more and more prominent. Finally, the cells begin to collapse and the coleoptile shrivels from the apex downwards. It is on the average recognizable for 30 days.

Growth of the coleoptile is not due to the presence of a meristem. With absorption of water, the preformed embryonic cells commence to elongate and to vacuolate from the apex downwards, the starch disappearing as the vacuolization proceeds. (Priestley and Tetley, 1927; Avery, 1928.)

When the tip of the coleoptile has passed the ground level, it splits into 2 lobes and through this split there emerges the first of the foliage leaves, followed subsequently and rapidly by the second, third, and fourth. Meantime, the node of the first true leaf begins to thicken and in a short time there emerge the first of the adventitious roots, usually a whorl of 4. The later formed adventitious roots develop from the nodes above. Unlike wheat, tillers do not develop until the plant is beyond the seedling stage. In all varieties, also, the number of tillers is fewer than in wheat.

As the seedling develops the internal structures already noted in the embryo become clearer. The cells of the first (or second) inter-node enlarge and differentiate, and growth in length takes place from the meristem immediately above the coleoptile plate. This whole region is a region of transition. There is a large pith and a circle of bundles, more or less alternately exarch and endarch in structure, towards the periphery. The pericycle and the endodermis are both prominent.

The way in which the vascular bundles of the coleoptile are supplied has already been noted. At the second (or third) inter-node (above the insertion of the coleoptile) elongation takes place by means of an intercalary meristem at its base. There is further a rather wide cortex, indefinite and poorly defined transition bundles, and a sheath of almost continuous meristematic cells containing some differentiated phloem and xylem. This sheath is believed by Avery (1930) to be pericyclic in origin. The succeeding inter-nodes are normal.

**CHROMOSOME NUMBERS AND KARYOLOGY.**—In 1915, Kuwada stated that the haploid chromosome number in Maize varied from 9 to 12. He suggested that maize might be a tetraploid plant and regarded 12 as the original number. Later (1919), he concluded that the basal numbers were 10 (haploid) and 20 (diploid). Deviations, however, occurred. In "Sugar Corn", "Black Mexican" and "Early Eight Sugar Corn", the average haploid number was twelve. The higher number also occurred in certain hybrids.

The conclusion that 10 is the basal number has since been confirmed by Longley (1924), Kiesselbach and Petersen (1925), Fisk (1925), Reeves (1925), Randolph (1928) and others.

That deviation from this basal number occurs has also been established. Fisk (1927) found somatic chromosome numbers varying from 20 to 23 (in "Black Mexican"), the number of bivalents in this variety varying in one plant from 9 to 11. Longley (1927) reported the occasional presence of supernumerary chromosomes in "Golden Bantam" and "Stowell's Evergreen" and more



frequently in "Black Mexican" and four other varieties. Randolph (1928) also found plants with more than the typical number in "Black Mexican" and "Golden Bantam", "New York State Flint" and "Hall's Nugget", and in

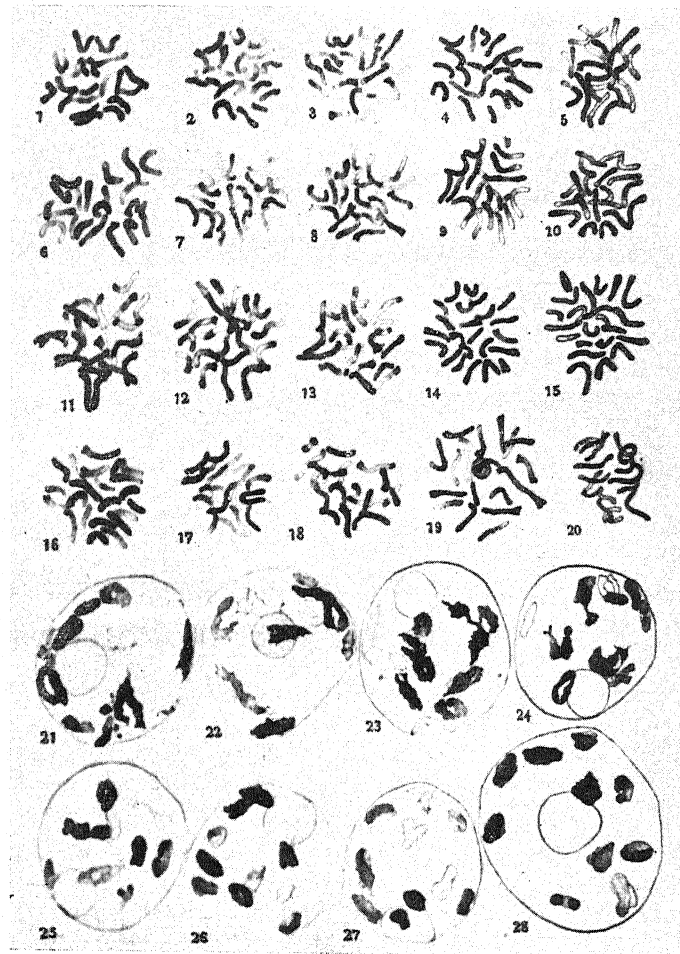


FIG. 173.—Chromosomes of *Zea*.

- 1-13. Root tip mitoses showing 20 chromosomes.
14. Ditto with 23 from Black Mexican.
- 15, 16. Black Mexican with 22.
17. Yellow flint with 19 chromosomes.
18. Tall floury with 20 chromosomes.
19. Dwarf floury with 19 chromosomes.
20. As in Figure 17, segmentation incomplete.
21. Diakinesis in Evergreen Sweet with 10 bivalents and 1 small rounded body.
- 22-24. As in Figure 21, 10 bivalents only.
25. Later diakinesis, 10 bivalents.
26. As in Figure 25 from Golden Glow Yellow Dent.
- 27, 28. As in Figure 25, Crosby Sweet. (After Fisk.)

seven genetical cultures. The numbers ranged from 21 to 28, and variation in different individuals was characteristic of these exceptional cultures.

Longley (1927) found the supernumerary chromosomes to resemble in size and shape the smallest of the normal chromosome set. He studied in detail the distribution of one supernumerary chromosome. At the first division, it goes undivided to one or other of the poles; at the second, non-disjunction occurs in varying percentages. In microspore mother cells, this variability ranged from 0 to 100 per cent.; in megaspore mother cells, it was approximately 26 per cent.

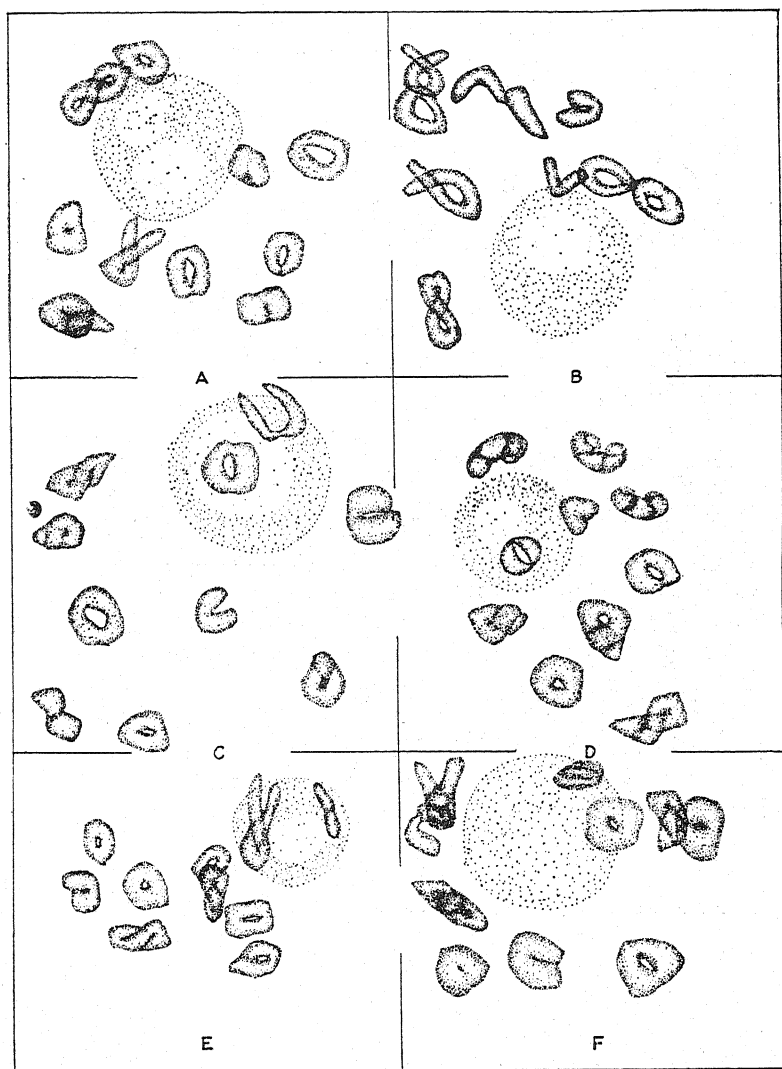


FIG. 174.—Diakinesis in the microspore mother cells of *Zea mays*, showing characteristic shapes assumed by the 10 bivalent chromosomes: A, Golden Bantam sweet corn; B, Black Mexican sweet corn; C, Red x Crosby; D, Wichita flint; E, Hybrid Ah-645; F, Country Gentleman sweet corn. (After Longley.)



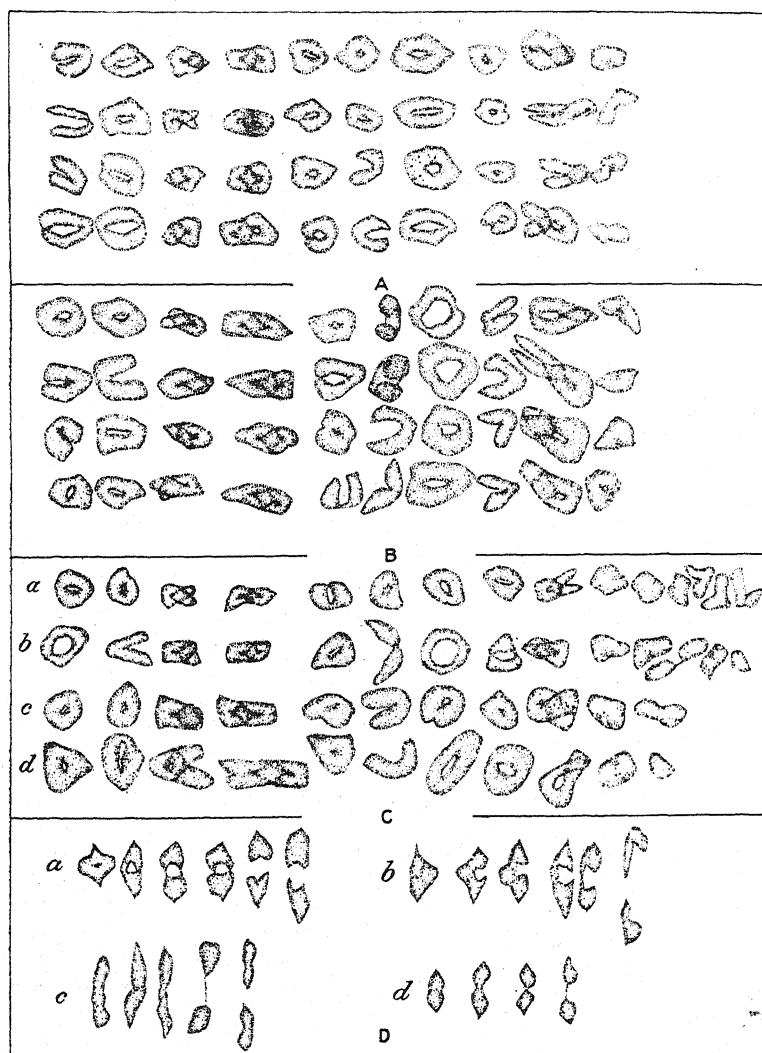


FIG. 175.—Bivalent chromosomes of maize: A, Four chromosome sets from hybrid Ah-645-1748, arranged to show the similarity of chromosome shapes in four microspore mother cells of the same plant; B, four chromosome sets from hybrid Ah-645-1751; C, *a*, a chromosome set from a plant of Black Mexican sweet corn with 15 bivalent chromosomes; *b*, a similar set from a sister plant with a univalent and 13 bivalent chromosomes; *c*, a set from a third sister plant with 11 bivalent chromosomes; *d*, a chromosome set from Country Gentleman sweet corn with a univalent and 10 bivalent chromosomes; D, chromosomes from heterotypic metaphase plates of microspore mother cells, showing the region of fibre attachment: *a*, Stages in the division of chromosomes with central fibre attachment; *b*, stages in the division of chromosomes with subterminal but no central fibre attachment; *c*, a larger chromosome with terminal fibre attachment; *d*, a smaller chromosome with terminal fibre attachment. (After Longley.)

Further, pollen viability seemed in no way affected by chromosome numbers. On the other hand, embryo-sac mother cells with 2 supernumerary chromosomes were tended to be eliminated.

Humphrey (1933) thereafter studied 19 forms, including a series of genetic cultural types. With two exceptions, 10 haploid and 20 diploid chromosomes were found. The exceptions were Emerson's strain tester A (aCRLG) with 11 and 22; and Bantam's "Evergreen" with 10 and 22 to 26 chromosomes respectively.

In the extra-chromosomal plants, 20 chromosomes were present which appeared to be similar in form to those of the typical complement. The additional units

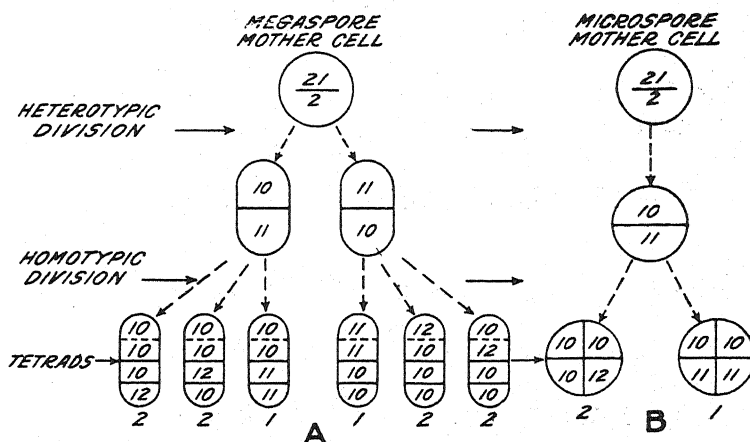


FIG. 176.—Diagram showing distribution at meiosis of  $21/2$  chromosomes to the four cells of a tetrad: A, Megaspore mother cells. The first division gives two cells, one with 10 and the other with 11 chromosomes. The second division gives six types of tetrads, two (see A-1) in which the division of the eleventh chromosome is normal and four (see A-2) in which there is nondisjunction of the two halves of the eleventh chromosome; B, microspore mother cells. The first division gives two cells, one with 10 and the other with 11 chromosomes. The second division gives two types of tetrads, one (see B-1) in which the division of the eleventh chromosome is normal and one (see B-2) in which there is nondisjunction of the two halves of the eleventh chromosome. (After Longley.)

could be identified on the basis of their unusual form and staining reaction. At meiosis, these units were usually independent of the bivalents, and their arrangement and distribution very variable.

Humphrey (l.c.) further noted that in the 26-chromosome plants of "Bantam Evergreen", there appeared to be a greater number of short chromosomes than in the normal plants. Although the relative lengths and thickness of the chromosomes appeared to be constant in any one culture, certain forms showed variation when compared with one another. Humphrey (1933) also states that the extra chromosomes do not appear to be fragments, and that their behaviour at mitosis is normal.

Avdulov (1933) studied in detail six 20-chromosome individuals of normal "Black Mexican" and also the karyotype present in individuals with 22 to 26 and

28 and 32 chromosomes respectively. He found in every type that an identical set of 20 chromosomes was present. The supernumerary chromosomes when present did not resemble any of the normal set, had no satellites and usually possessed no constrictions. As they appear to exert no influence on the hereditary constitution of the plants, Avdulov, contrary to the opinion of others, came, therefore, to the conclusion that they could not have originated from any of the existing chromosomes. No other plant with such accessory chromosomes is known.

Kuwada (1919) reported that maize chromosomes were of two types, a long and a short series. Now *Euchlaena* has 10 haploid chromosomes which are long, and *Andropogon* 10 which are short. He accordingly regarded the presence of a long and a short chromosome set in Maize as supporting the theory of its hybrid origin.

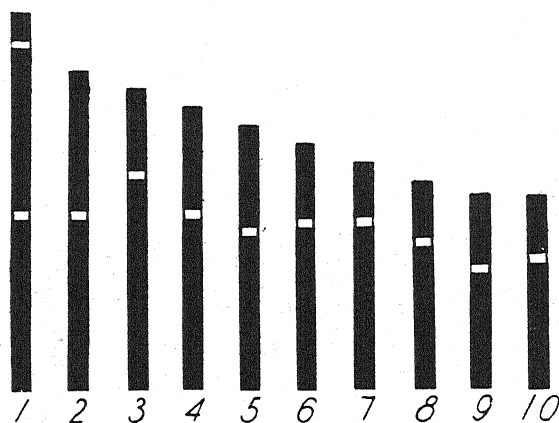


FIG. 177.—Diagram drawn to scale of the ten chromosomes of maize. (After McClintock.)

Hance (1921), however, did not consider that Kuwada's methods were such as to prove that the sizes of the maize chromosomes correspond to the types of *Euchlaena* and *Andropogon* respectively. Kiesselbach and Petersen (1924) found no evidence in support of Kuwada's contention. Randolph (1927) makes the note: "significant differences in the length of the members of bivalent chromosomes were not observed;" Fisk (1927) states: "such a separation into two distinct classes of long and short chromosomes has not been found possible."

Longley (1927) described the 10 bivalent chromosomes at diakinesis as six double *V*s, two double *J*s, a figure 8, and a small chromosome with no easily described shape.

Later, McClintock (1929 b) described and figured the whole complement (Fig. 179). Each can be identified on the basis of its structure. The longest (now known as No. 1) is more than twice as long as the shortest (No. 10: Fig. 179). The point of attachment varies, but is neither terminal nor strictly median (Avdulov, 1933). Thus, in number 5, the chromosome is divided by the attachment into two almost equal arms; in number 8 the division is such as to give a long arm three times as long as the short; in number 6, the long arm is about

six times as long as the short. To this chromosome (No. 6) the nucleolus is attached at a fixed point on the short arm next to the satellite.\*

Darlington (1934) studied the origin and behaviour of the chiasmata in a number of interchange types and three trisomic forms (trisomic for chromosomes 3, 2 and 1).

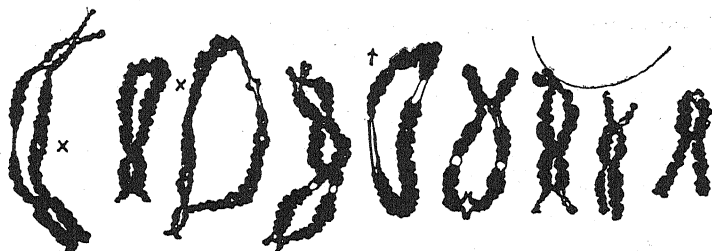


Fig. A

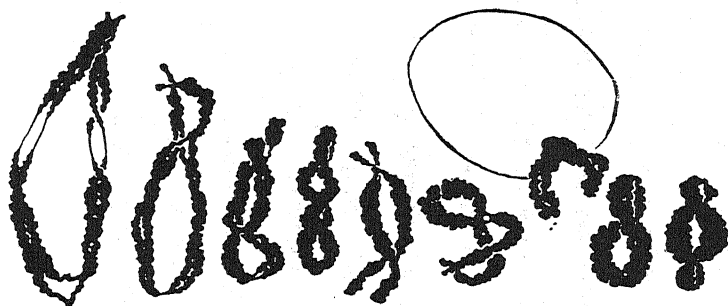


Fig. B

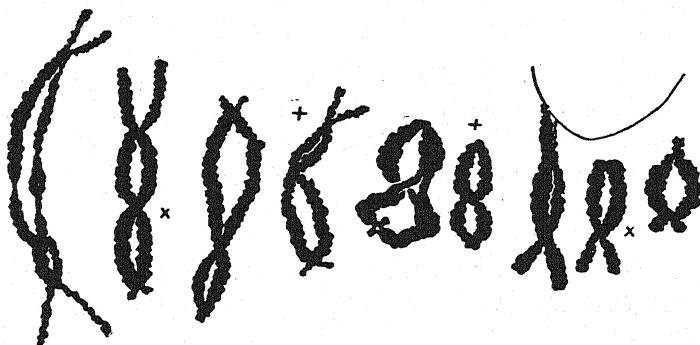


Fig. C

FIG. 178.—Maize chiasmata. Successive stages of late diplotene in plant heterozygous for an interchange between chromosomes 8 and 9 (105 b 5). The spindle attachment chromomeres are still distinguishable in the early stages. The 6th chromosome is attached to the nucleolus. The average number of chiasmata is 2.7 (49.5 per cent. having 2). Terminalization is low. (After Darlington.)

\* The presence of knobs on 9 of the 10 chromosomes was also demonstrated.

The average number of chiasmata at prophase of meiosis in the pollen mother cells was 2.7 and was only slightly reduced by fusion in terminalization. The frequency of chiasmata in rings of four of known constitution and in the nucleolar chromosome indicated that the relation of chiasmata to length was a non-linear one. The inferred chiasma frequency of individuals made it possible to predict (on the modified chiasmotype hypothesis) what should be the total corrected crossing-over length of each. The length so far mapped genetically amounts to 46 per cent.

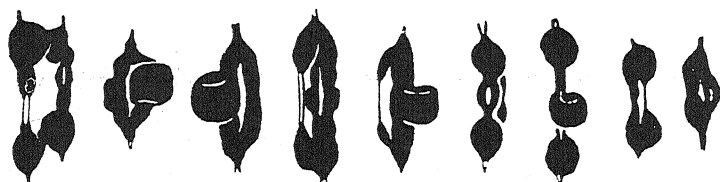


Fig. 1

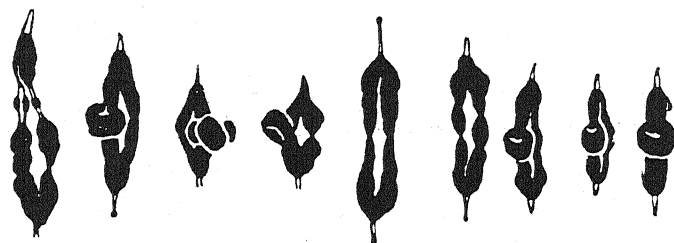


Fig. 2

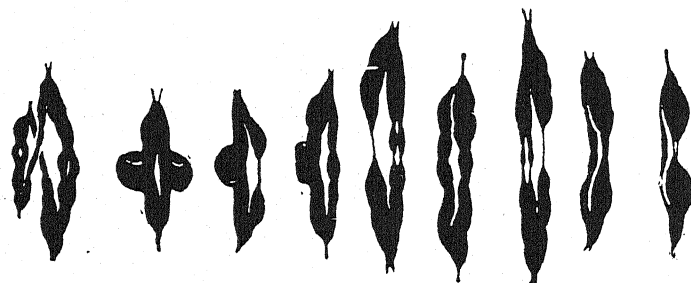


Fig. 3

FIG. 179.—Side view of first metaphase in plant 105b5. Three nuclei showing the ring of four, nondisjunctional in 1 and 2, disjunctional in 3. (After Darlington.)

of this estimate. In the trivalents of the trisomic plants, the chiasma frequency was higher than in the corresponding bivalents.

In 1926, Randolph and McClintock published a note on polyploidy in *Zea*. Later, Miss McClintock (1928) studied in detail the triploid type, and reported on the result of reciprocal crosses with diploid forms. In the triploid, 10 trivalents were frequently shown, but there was a tendency for the extra set of chromosomes to be dissociated from their homologues at diakinesis and metaphase, thus

forming 9 trivalents, 1 bivalent and 1 univalent or 8 trivalents, 2 bivalents and 2 univalents, etc. In F<sub>1</sub> crosses between diploid and triploid, there was a decided selection against extra chromosome carrying male gametes and a less obvious selection against extra chromosome carrying eggs. It is also of interest to note that the presence of extra chromosomes (apart from the triploid which is vigorous) was associated with a decrease in size and vigour, but did not produce any particular recognizable characters.

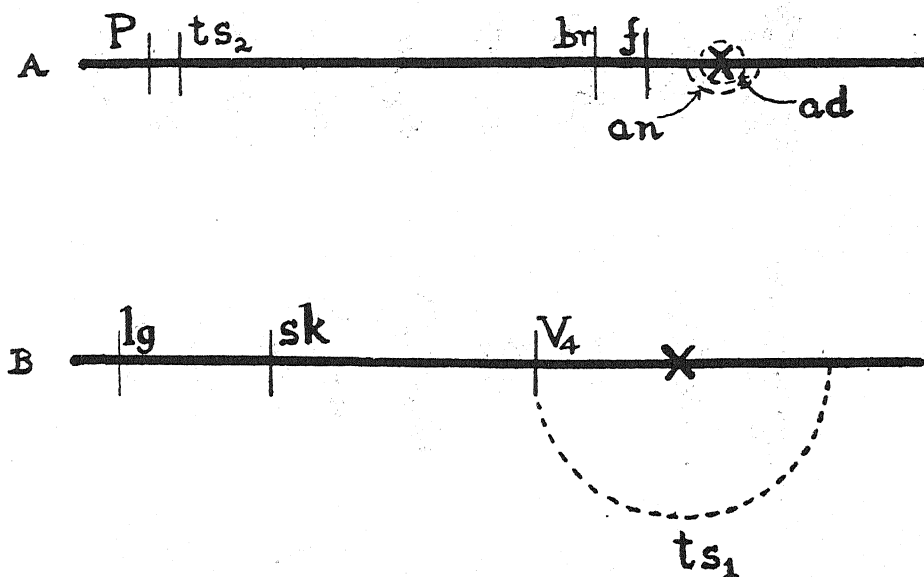


FIG. 180.—Chromosomes involved in the interchange in Semi-sterile 1.

- A. Map of chromosome 1 (*P br*) showing the position of the assumed break (X) in relation to six genes with which semi-sterility was tested.
- B. Map of chromosome 2 (*lg v<sub>4</sub>*) showing the position of the assumed break (X) in relation to four genes with which semi-sterility was tested. (After Brink and Cooper.)

In addition to these unbalanced forms, occasional failure of pairing has been noted in inbred diploids (Randolph, 1928). Beadle, in 1931, discovered a recessive factor which is "asynaptic" in its action. As a consequence the chromosomes fail to pair; 0 to 2 bivalents usually develop but rarely complete pairing is found. At the first division, the chromosomes are irregularly scattered but at the second they divide. Diploid restitution nuclei may form. The behaviour in the embryo-sac appears to be similar, since half of the progeny when the type is crossed with normal pollen are triploids. Failure of the spindle to develop (Beadle, 1932) also produces abnormal segregation, and is genetic in nature.

Of the genera allied to *Zea*, *Euchlaena mexicana* has 10 haploid chromosomes; *Euchlaena perennis* 20; *Tripsacum dactyloides* 18 and 36 (tetraploid); *Coix lachrym-jobi* 10. (Longley, 1924.)

**STRUCTURAL HYBRIDS.**—Brink (1925-1927) discovered a strain of maize which was semi-sterile (known as semi-sterile 1, now as T1-2a).<sup>\*</sup> This strain when selfed or crossed with normal plants, produces fertile and self-sterile progeny in the ratio of 1 : 1 (Brink and Burnham, 1929). Half the pollen grains and half the embryo-sacs, however, abort. Since the condition nevertheless is transmitted, some of the functional gametes must carry the complex responsible, and breeding tests indicate that exactly half the gametes are of this nature. Further, one half of the progeny of self-pollinated self-sterile plants are of a new type. Though indistinguishable outwardly from normal, they give rise, when intercrossed with normals, to 100 per cent. self-steriles (Brink and Burnham, 1929). Such types are termed x-normal, in contrast to the fully fertile forms, known as O-normal. Cytological examination of semi-sterile 1 by Burnham (1930) indicated

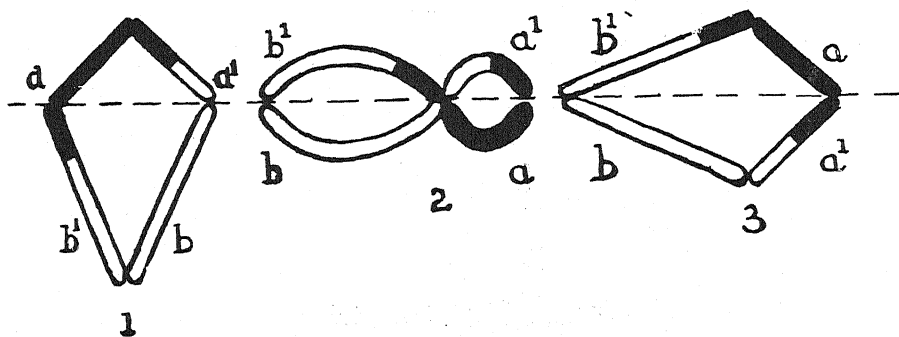


FIG. 181.—Diagrammatic representation of the assumed constitution of the chromosome ring in semi-sterile 1 (T1-2a) plants on the basis of segmental interchange. One end of chromosome *a* has interchanged with an end of chromosome *b*. The ring is oriented on the equatorial plate so that, 1, adjacent chromosomes of the same size, 2, alternate chromosomes and 3, adjacent chromosomes of unlike size pass to the same pole. (After Brink and Cooper.)

the presence of 8 bivalents and a ring (rarely a chain) of 4 chromosomes. By testing with known genes of the nine linkage groups, Brink and Cooper (1931) found that the chromosomes involved in the ring must be those of the *B-lg* group (the second from the longest) and the *P-br* group (the longest chromosome).

On the basis of Belling's segmental interchange hypothesis, Brink (1930) and Brink and Burnham (1929) postulate that a terminal segment of one of the *P-br* chromosomes must have interchanged with a terminal segment of one of the *B-lg* chromosomes. The approximate position of this interchange is indicated in the Diagram 180. On the assumption that the homologous ends of the 4 chromosomes attract each other, a ring must accordingly be produced.

In the diagram, Fig. 181, three positions of the ring are shown, such that in 1, adjacent chromosomes of the same size; in 2, alternate chromosomes; and in 3, adjacent chromosomes of unlike size will pass to the same pole. If alternate

<sup>\*</sup> The capital letter T is now used as a general designation of interchanges; the numbers indicate the chromosomes involved; the small letters are added if there be more than one interchange between the same chromosomes.

chromosomes,  $ab$  and  $a^1b^1$ , pass to the same pole, functional gametes will result, each daughter nucleus receiving a full complement of the genes involved. When this happens half of the gametes will incorporate chromosomes  $a$  and  $b$ , the other half the interchange chromosome  $a^1$  and  $b^1$ . On the other hand, if adjacent chromosomes pass to the same poles, each daughter nucleus will be deficient in part of a segment, and as a consequence abort, owing to the total absence of certain of the genes. Cytological examination of the material indicates that this takes place. Further, the fact that 25 per cent. of the offspring of selfed semi-sterile 1 (T1-2a) plants are semi-sterile x-forms is also explicable on the above hypothesis. Such plants are homozygous for the double translocation ( $a^1b^1$ ,  $a^1b^1$ ).

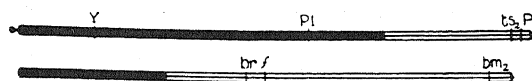


FIGURE 1. Chromosome map of the segmental interchange involved in semi-sterile 5.

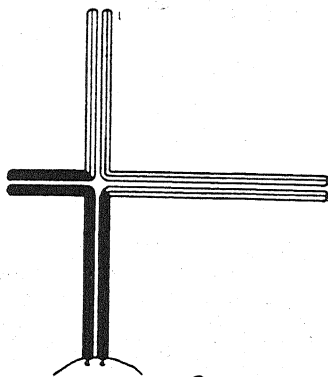


FIGURE 2

FIG. 182.

1. The chromosomes involved in semi-sterile 5.
2. Diagrammatic representation of the cross-shaped figure found at early prophase in semi-sterile 5.

The chromosome in black, and attached to the nucleole corresponds to the Y-Pl linkage group. (After Brink and Cooper.)

A further series of semi-sterile forms has since been obtained. Semi-sterile 2 (T8-9a) (Burnham, 1930) is slightly more than 50 per cent. sterile. It exhibits at diakinesis 8<sup>11</sup> and a ring of 4. McClintock (1928 and 1931) and Creighton and McClintock (1931) have shown that the ring here involves the second smallest chromosome (No. 9, associated with *Cwx*) and the third smallest chromosome (No. 8). By inter-crossing with a strain of maize in which the ninth chromosome, carrying the linkage group *Cwx*, possessed a conspicuous knob at the end of the short arm, these authors were able to demonstrate the interchange and the approximate position of the break both cytologically and genetically.



Burnham (1930) demonstrated that the cross semi-sterile 1 (T1-2a)  $\times$  semi-sterile 2 (T8-9a) gave rise to progeny which were more than 75 per cent. sterile. These hybrids had 6<sup>11</sup> plus two groups of 4 chromosomes. In semi-sterile 3 (T1-7a), one of the chromosome pairs involved is probably the same as semi-sterile 1. The chromosomes concerned must therefore be either the Pbr group or the Blg group. The combination of semi-sterile 3 therefore produces hybrids which are less than 75 per cent. sterile and exhibit, according to expectation, 7<sup>11</sup> plus a ring of 6 chromosomes.

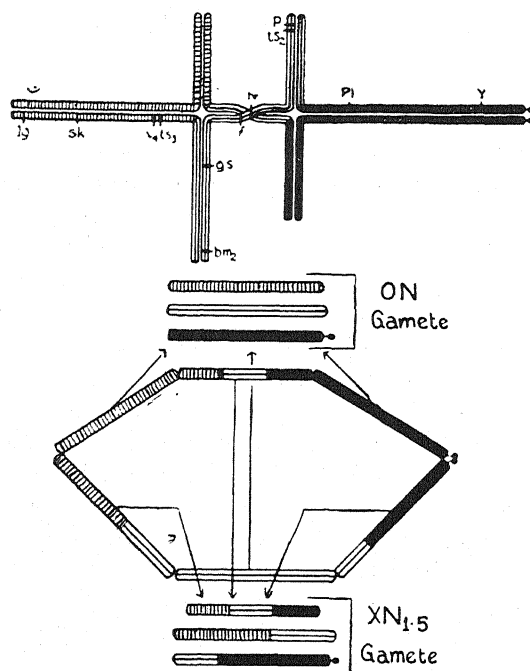


FIG. 183.—Diagrammatic representation of the origin of the X. normal 1.5 type through crossing-over in the interstitial segment of the ring of six chromosomes found in hybrids between semi-sterile -1 and -5. (After Brink and Cooper.)

In semi-sterile 4 (T2-5a) Rhoades (1931) has shown genetically that the *lgB* and *pr-v*<sup>2</sup> chromosomes are involved. The interchange is approximately an equal one, and the evidence indicates that it took place towards the left end of both chromosomes, close to the *ts* gene in the case of the *lg-B* chromosome, but uncertain in position in the case of the *pr-v* chromosome. Since the *b-lg* chromosome is common to both, the hybrid of semi-sterile 1  $\times$  semi-sterile 4 exhibits 7<sup>11</sup> and a ring of 6 chromosomes.

Brink and Cooper (1931, 1932) have studied a further type, semi-sterile 5 (T1-6a), involving the linkage groups of the *P-br* and *Y-Pl* chromosomes. The *Y-Pl* chromosome possesses a satellite and is attached at that end to the nucleolus. The interchange appears to have taken place at the opposite end to the satellite of this chromosome, the sequence being nucleole—*Y-Pl*—break (Fig. 182).

Again, owing to the presence of *P-br* in both, the cross of semi-sterile 1 × semi-sterile 5 exhibits 7<sup>11</sup> and a ring of 6. (Fig. 183.)

Burnham (1930) and McClintock (1931) have shown that very low sterile forms with 21 chromosomes may be derived from semi-sterile types owing to irregular (3 to 1) disjunction. Burnham (1932) has also studied a low sterile form—Tr-6b—(25 per cent. sterile) with 20 chromosomes in which 8<sup>11</sup> plus a chain of 4 chromosomes regularly occurs. By suitable inter-crossing, the chain has been proved to involve the satellite chromosome *Y-Pl* and the *P-br* chromosome group, which is the longest in maize. The interchange involved is short, and the hypothesis is advanced that a gamete deficient for but a small part of the satellite chromosome need not necessarily abort. As a consequence, a low sterility of approximately 25 per cent. results.

A number of other forms have since been studied (Anderson, 1934; Anderson and Clokey, 1934; Burnham, 1934, a, b and c; Clarke and Anderson, 1934; McClintock, 1933), and many additional types have also been obtained by X-ray treatment. The frequencies of these interchanges are approximately proportional to the lengths of the different chromosomes (Anderson, 1935). The value of these interchanges types has also been further demonstrated by Brink and Cooper (1935) who, utilizing a strain of maize carrying two reciprocal translocations, obtained configurations clearly indicating that the genetic crossing-over involved exchange of segments between corresponding chromosomes.

Rhoades (1931, 1933) has reported an unusual condition of male sterility. The strain was obtained by Emerson in Peru and was completely male sterile. When crossed to a normal form, the F<sub>1</sub> plants were all male sterile and showed no signs of female sterility. Cytological examination proved that 10<sup>11</sup> were present and that the divisions were normal. Degeneration of the pollen usually took place before the first vegetative division. There was, however, a pronounced difference between the cytoplasmic elements present in normal individuals compared with those of male steriles. Replacement of the chromosomes in the male-sterile plants with chromosomes known to be devoid of sterility had no apparent effect on the degree of sterility and no linkage was found between this sterile condition and the known linkage groups. No transmission of the male sterility through the pollen of partially sterile plants took place, nor had the nature of the pollen parent any demonstrable effect upon the expressions of male sterility. As there was also no indication of virus disease being present, Rhoades concluded that the egg-cytoplasm must play the chief rôle in the expression of the character.

If this be the explanation, the case is totally different from other instances known to be due to genetic factors. (Eyster, 1921; 1930; 1931; Singleton and Jones, 1930; Beadle and McClintock, 1928; Beadle, 1932.) The last author has now isolated 15 genes which may produce this effect.

CLASSIFICATION.—Sturtevant (1899) divided *Zea Mays* into the following series of "species-groups" or "sub-species".

1. *Zea Mays tunicata*, pod maize.

Here the kernels are enclosed in the bracts and the ear in the husks. All shapes, types and colours are present. (There is evidence that the podded condition is one of imperfect dominance.)

2. *Zea Mays everata*, "pop" maize.

Ears generally small, 8- to 16-rowed; endosperm mainly corneous; pericarp tough; grains with marked popping qualities, generally small, rounded or pointed; all colours present.

3. *Zea Mays amylacea*, soft maize.

Ears long, 8- to 12-rowed; grains with no popping qualities; endosperm soft; shape like flint maize; all colours present.

4. *Zea Mays saccharata*, sweet maize.

Plants generally small to intermediate; ears medium to long; grains more or less wrinkled; endosperm horny; starch content low; all shapes and colours present.

5. *Zea Mays Indurata*, Flint maize.

Plants generally medium to tall; ears usually long and slender; 6- to 12-rowed; grains more or less rounded; endosperm starchy within, surrounded by a horny envelope of variable thickness; all colours present.

6. *Zea Mays indentata*, Dent Maize.

Plants medium to very tall; ears relatively short and thick; grains flat with apex indented; endosperm with a central starchy column surrounded by a corneous cylinder; all colours present.

Several other types have been described, e.g., *Zea Mays hirta*, with excessive hairs on leaves and sheaths; *Zea Mays japonica*, with striped leaves; *Zea Mays gracillima*, with dwarf habit; *Zea Mays amylea-saccharata*, with the lower half of the grain starchy, the upper corneous. The form *Zea Mays canina* was reported as a wild species from Mexico. It is now known to be a segregate from natural crosses between Maize and Teosinté.

The above classification is a purely artificial one, based upon one or a small number of characters. Further, certain varieties could be grouped in more than one of the subdivisions.

Genetical analysis has established the fact that all maize varieties are markedly heterozygous. Any constant variety could be termed a "balanced" heterozygous form. Inbreeding reveals the actual composition. Accordingly, the only satisfactory treatment is to recognize that maize is a highly variable complex species (or genus), whose primary characteristics are now indefinable through hybridization. As genetic analysis proceeds, it will be possible to state what the probable expressions of the various characters are, and so ultimately to define the primary characteristics. "To integrate it is necessary to differentiate."

**XENIA IN MAIZE.**—The term Xenia means "a gift of hospitality". It is applied botanically to the phenomenon which is best illustrated in crosses between certain varieties of maize—namely, the immediate effect of cross-pollination on the endosperm of the plant. To take an example. If we fertilize a variety whose endosperm is white with pollen from a variety whose endosperm is yellow, the resulting grains on the ear of the white variety will be yellow, not white. Here we have the effect of the foreign pollen impressed immediately on the endosperm of the grain. For many years after the discovery of Xenia, no satisfactory explanation of the phenomenon was advanced. Later, the discovery of double fertilization in the embryo-sac of angiosperms afforded a key to its solution. The pollen tube discharges not 1 but 2 nuclei. The first fertilizes the

egg; the second fuses with the polar nuclei to form the primary endosperm nucleus—the parent of all the nuclei of the endosperm. The pollen grain therefore brings a definite contribution to the endosperm. (Correns, 1899; Guignard, 1901; De Vries, 1910; Weatherwax, 1919.) Now breeding experiments have established the fact that yellow endosperm is dominant over white. In our example, the factor for yellow is introduced into the primary endosperm nucleus along with the second male nucleus. There results a hybrid endosperm whose nuclei must contain the factor for yellow. Since yellow is dominant, the hybrid endosperm exhibits the dominant character. All grains accordingly are yellow.

In recent years, the phenomenon of Xenia has been studied in great detail. Following East (1913), we may summarize the position in the author's own words.

1. "When two races differ in a single visible endosperm character in which dominance is complete, Xenia occurs only when the dominant parent is the pollen parent." *e.g.*, Yellow pollen on a white silk produces Xenia, but white pollen on a yellow silk does not produce Xenia. In the reciprocal cross the introduced factor is not dominant. Hence the endosperm retains its yellow character and does not become white.

2. "When the two races differ in a single endosperm character in which dominance is incomplete, or when they differ in two characters, both of which are necessary for the development of the visible difference, in both of these cases Xenia occurs when either parent is male."

Normally, a dominant character in the endosperm is not suppressed by two doses of the recessive character. Thus, the dominant character starchiness is expressed whether the constitution of the endosperm be *SuSuSu* or *Suusu*. This is not always the case. Thus in the cross flinty  $\times$  floury, the endosperm is *FFf* and naturally flinty in character; but in the reciprocal cross, floury  $\times$  flinty, the endosperm is *ffF* and floury in character. The dominance of *F* over *f* is insufficient to produce flintiness in the presence of the two recessive factors for flouriness. This is true also for certain aleurone colours.

In addition to the above, there are certain obscure cases of Xenia which have not yet been satisfactorily explained. The further complication of hetero-fertilization has already been referred to.

**BREEDING AND HYBRIDIZATION.**—The older commercial varieties of maize and some of the recent were the product of mass selection. Such selection is effective only within limits, and the method is one which maintains rather than improves the standard of the type. Nevertheless, much work has been done in correlating yield with specific characters, and so facilitating selection. The correlations obtained, however, have not proved too satisfactory, although certain characters such as general vigour in relation to locality, the tendency to produce two ears in place of one, ears that are long and heavy, with heavier cobs, fewer rows, fewer kernels per inch and lower shelling percentage, tend to be associated with high yield (Richey, 1927).

The well-known "ear-to-row" method of selection—introduced by Hopkins at the Illinois Experimental Station in 1899—was developed in order to estimate the potentiality of each parent plant. Various modifications of the method have been employed, and it has been used successfully in the improvement of certain specific characters.

With the advance in genetical knowledge of the maize plant, breeding by selection has been in part discarded, and methods have been adopted which attempt to rebuild the constitution of the plant, so as to incorporate a majority of the desirable factors from the best material available. This is effected, 1/ by inbreeding and 2/ by re-combining the products.

Since maize is mainly cross-pollinated, the varieties are heterozygous. Inbreeding induces homozygosity resulting in the isolation of markedly uniform strains, which, however, may differ in many respects from one another. All tend to show reduction in yield as such though not necessarily in vigour. Many strains, indeed, though lower yielding than the parental stock, are not only markedly uniform but otherwise desirable. Others exhibit undesirable features owing to the combination of homozygous recessives; many are lethal. Recombination of these strains restores the vigour and may result in types more desirable and higher in yield than the originals (Hutchinson and Wolfe, 1917). This hybrid vigour or heterosis is believed to be genetic, the result of recombining certain particular factors. As these factors are linked with others and may be distributed in varying combination over all of the 10 chromosomes, the production of a strain homozygous for a considerable number of such factors, though theoretically possible, is highly improbable. (Jones, 1917.)

In the study of heterosis, however, it has been tacitly accepted that the vigour exhibited by hybrid maize affects the plant as a whole. A number of the earlier investigators clearly indicated that hybridity increases the size of the seed. This was stressed by Carrier in 1919. Other investigators (*e.g.*, Collins and Kempton, 1913; Wolfe, 1915; Jones, 1918; Kiesselbach, 1922) also found definite increases in the weight of crossed compared with normal grain. East and Hayes (1914) made the vague statement that crossing inbred strains increases the "amount and rapidity of assimilation as expressed by cell division". Later, East and Jones (1919) not only showed that embryo and endosperm may be heavier but that there is an increase in the germination capacity of hybrid seed. Ashby (1930)\* undertook a critical analysis of the physiological differences between an  $F_1$  generation and its two inbred parents. He found that the hybrid did not differ in the least from its more vigorous parent as regards relative growth rate, cell size, photosynthetic activity or the time of flattening of the sigmoid curve of growth. The only physiological differences noted were, 1/ an increased percentage germination on the part of the hybrid, and 2/ a greater initial weight of the hybrid embryo, which gave it an advantage which was maintained throughout the period of growth. There is therefore no real difference after germination between the growth of a hybrid and that of the more vigorous parent. The heterosis exhibited by the hybrid "is due to some process between the fertilization and the setting of the seed". Of equal importance was the discovery that the relative growth rate was apparently inherited as a dominant Mendelian factor.†

\*Ashby's conclusions have been challenged by Lindstrom (Amer. Nat. 69: 311-312. 1935) and also by East (Genetics 21: 375-397. 1936).

† See also Ashby, Ann. Bot. 46: 1932; N.S. 1: 1937; Amer. Nat. 70: 1936. In these papers Ashby clarifies his position. From data on Maize, Tomatoes, Cucurbita, Guinea-pigs and Pigs, he concludes that heterosis acts through *capital* in the embryo and not *rate of interest*. This increase in capital is resident in the apical primordia of the embryo, not in the stored-food or seed size. Further, this conclusion is no solution of the problem of heterosis: "it merely refers the problem back to the beginning of the life-cycle."

In recombining two inbred strains it is as yet impossible to forecast the nature of the progeny. The method of trial and error is the only one available. Double-crossing as a consequence has been introduced. In this method two strains of selfed-lines are first inter-crossed, and the two F<sub>1</sub> generations are then combined. This procedure tends to increase the chances of uniting in one stock a large number of desirable features, and at the same time ensures heterosis. Similarly, the inter-crossing of a number of strains has been employed with success. Recently, a modification of these methods has been employed. The pollen parent only is inbred, and the selected strain is then inter-planted with a standard variety, which is detasselless as it develops. A large bulk of hybrid seed is thereby obtained from the commercial variety, and at the same time the selected pollen parent is

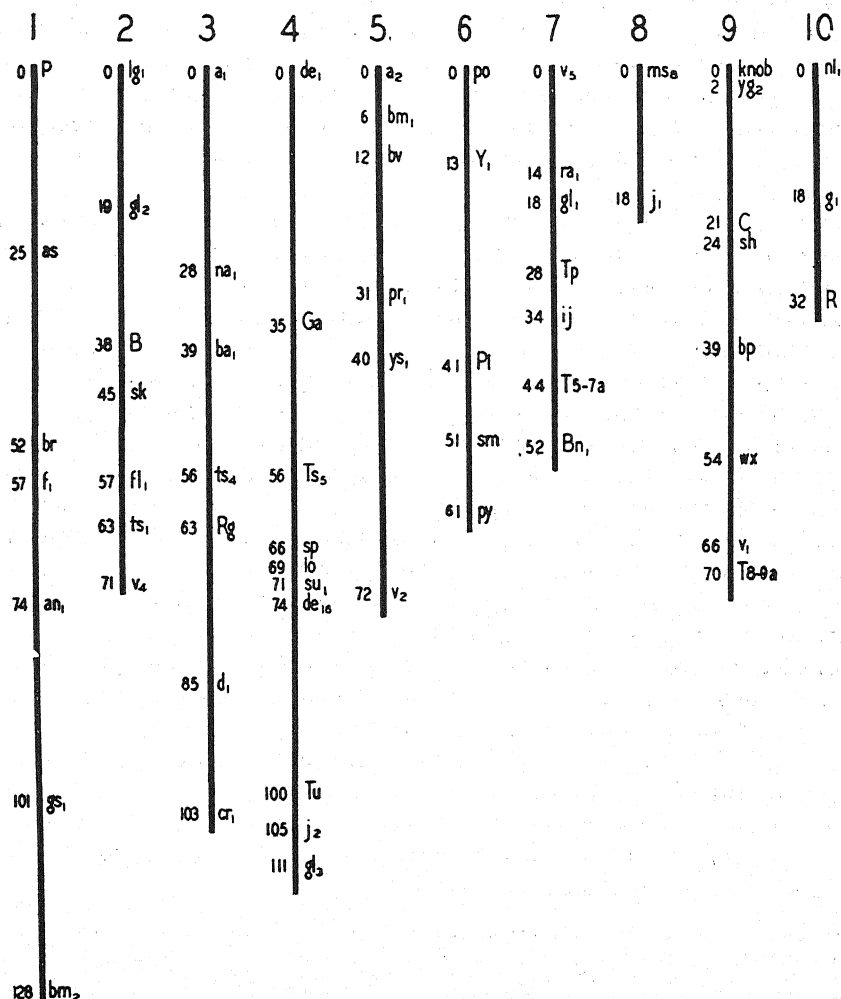


FIG. 184.—Linkage map of the ten chromosomes of *Zea Mays* showing the loci of those genes whose position can be determined with reasonable certainty. (After Dr. M. M. Rhoades from data in Emerson *et al.*)



maintained in its original condition (Lindstrom, 1931). As a more precise knowledge of the chromosomes and the factors carried by them is obtained, the synthesis of types whose characters may within limits be foretold, is not impossible. At the same time, the mutant forms in maize are so numerous, and the recombinations possible so enormous, that the unexpected will always remain a factor in the situation.

Recently, the induction of mutants by irradiation has been attempted. The changes so induced affect both the chromosome structure and the genes themselves. The mutants produced, however, do not appear to be different in kind from those that spontaneously develop, but the rate is undoubtedly increased (Stadler, 1931).

Randolph (1932) succeeded in inducing polyploidy in maize by subjecting plants in the early embryonic stage to high temperatures for short periods. The time of heat application was so arranged that it coincided with the first cell divisions of the pre-embryo. As a consequence, in addition to aborted, scarred and defective grains and grains with mosaic endosperms, tetraploids were induced with a frequency of 2 to 5 per cent.

The tetraploid plants closely resemble the diploids in general features but the individual organs are larger. Cell size is also increased. Fertility, however, is decreased, the amount varying from 5 to 20 per cent. in different  $4n$  stocks. The tetraploid plants can be maintained in the field, and breed true for tetraploidy.

Hybrids between  $2n$  and  $4n$  exhibited marked incompatibility and were highly cross-sterile in both direct and reciprocal crosses. When the diploid was the seed parent, the amount of fertility (measured by the proportion of viable to non-viable seeds) was less than 0.5 per cent.; in the reciprocal cross the amount ranged from 3 to 5 per cent. The resulting progeny were mostly triploids.

Cytological examination of the tetraploid stocks showed that departure from the typical chromosome number ( $40$ ) occurred. This variation amounted to one or a few chromosomes more or less than  $40$ , but the variations had little or no effect on the phenotype.

At meiosis, chromosome association was almost exclusively in quadrivalents and bivalents, with usually 7 to 9 quadrivalents and 3 to 1 bivalents. Trivalents were rare. Irregularities in distribution were noted, sufficient to account for the inconstancy in chromosome number in the progeny (Randolph, 1935).

In the course of the above experiments, genetical studies of maize strains have been conducted very extensively. As a consequence, our knowledge of the factors underlying the expression of the characters and their relation to the chromosomes, is now more extensive in maize than in any other plant. It is, however, beyond our scope to discuss the detail. Recent reviews have been published by Lindstrom (1930), Emerson (1932) and Eyster (1934).

Generic hybrids of maize with *Euchlaena* and *Tripsacum* have been obtained. *Zea Mays* ( $n = 10$ )  $\times$  *Euchlaena mexicana* ( $n = 10$ ) occurs naturally in Mexico. It was, indeed, the discovery of these hybrids that focused attention on the relationship of *Zea* and *Euchlaena* and led to the conception of a hybrid origin for maize. (Harsberger, 1901.)

The hybrids are perfectly fertile; they resemble Teosinté more than maize; in the  $F_2$  generation they segregate into Teosinté forms, intermediates and maize-like forms. The inheritance of some of the characters has been followed in detail,

and the two species undoubtedly possess genes in common. (Collins, 1917, 1918; Collins and Kempton, 1920.) Both species have 10 chromosomes and pairing appears to be regular. Avdulov (1933), indeed, states that the chromosome complement in *Euchlaena* appears to be almost identical to that of maize.

More precise studies are now in progress. Making use of known genes linked with particular chromosomes in maize (*e.g.*, chromosome No. 9) and the semi-sterile form No. 2 (a translocation of chromosomes 8 and 9), and introducing into these maize stocks the *Teosinté* homologues of these chromosomes, Emerson and Beadle (1930), Beadle (1932) and Emerson and Beadle (1932) have studied the crossing-over that occurs both genetically and cytologically. The evidence so

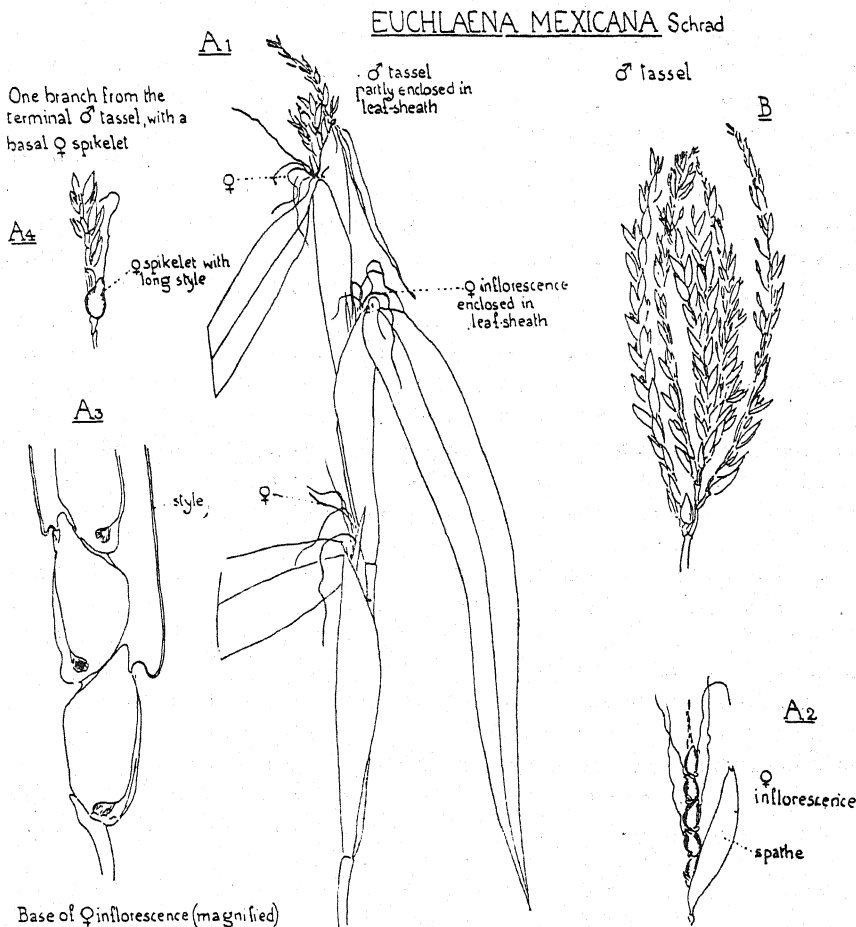


FIG. 185.—*Euchlaena mexicana* Schrad. Herbarium material of cultivated plants from Professor Weatherwax. A1, A2, A4 and B ( $\times \frac{1}{2}$ ), A3 (enlarged). A1, reproductive shoot with male and female inflorescences partially enclosed in leaf sheaths; A2, female inflorescence; A3, base of female inflorescence; A4, androgynous branch from the male tassel. B, a male tassel. (After Arber, *The Gramineae*, by permission of the Cambridge University Press.)



obtained from these and future studies should prove of great importance in the interpretation of crossing-over.

The perennial form of Teosinté (*E. perennis*) with 20 haploid chromosomes has also been hybridized with maize. Emerson and Beadle (1930) have obtained from the cross a fertile tetraploid hybrid with 40 chromosomes, due to doubling in the pollen only.

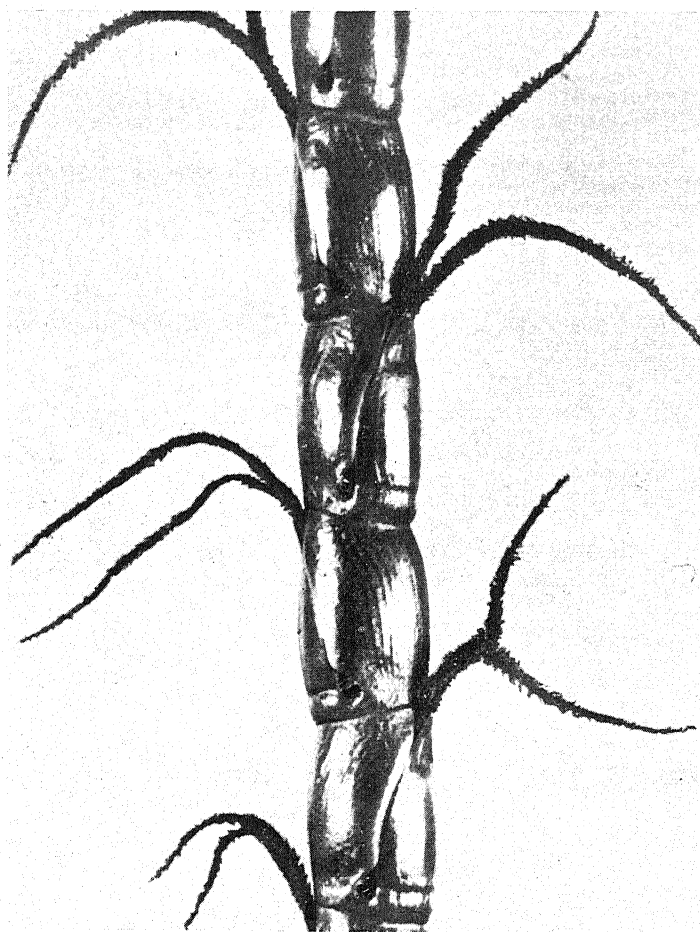


FIG. 186.—Pistillate spikelet of *Tripsacum*. (After Mangelsdorf and Reeves, by permission of the J. of Heredity.)

Hybrids of maize with *Tripsacum dactyloides*, one of the three indigenous species of *Tripsacum* in the United States, have been secured. In 1916, Collins and Kempton, in an attempt to cross *Tripsacum*  $\times$  *Zea*, secured "matroclinous" plants, perhaps the result of parthenogenetic development of the *Tripsacum* ovules. They also tried to hybridize *Tripsacum* with *Euchlaena* pollen but failed to do so, obtaining one plant with "patroclinous" characters which appeared to

be pure *Euchlaena*. Recently, Mangelsdorf and Reeves (1931) in an attempt to induce parthenogenesis in maize by the use of *Tripsacum* pollen, obtained a large number of true hybrids. Their success was due to the fact that they pollinated maize ears whose silks had been cut back to less than an inch in length.

Two types of *Tripsacum* were employed:—(1) a Connecticut variety with 72 chromosomes and presumably tetraploid; and (2) a Texas variety with 36 chromosomes. The hybrids secured with both types of pollen resembled the male *Tripsacum* parent more than the maize parent. This was more pronounced

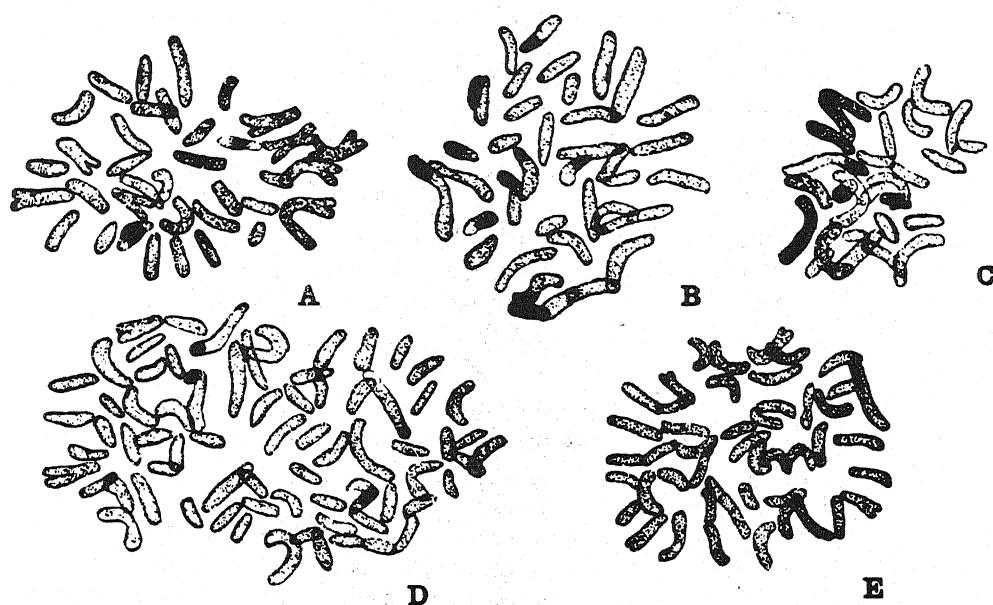


FIG. 187.—Somatic Chromosomes of *Tripsacum* and its Hybrids with Maize.

- (A) Texas *Tripsacum*: 36. (B) Endosperm of maize  $\times$  Texas *Tripsacum*: 38. (C) Embryo of maize  $\times$  Texas *Tripsacum*: 28. (D) Connecticut *Tripsacum*: 72. (E) Root-tip of maize  $\times$  Connecticut *Tripsacum*: 46. (After Mangelsdorf and Reeves, by permission of the J. of Heredity.)

in the case of the maize  $\times$  Connecticut variety whose pollen contributed 36 *Tripsacum* chromosomes than in the hybrid from maize  $\times$  Texas variety, contributing only 18 *Tripsacum* chromosomes.

The hybrids had 28 and 46 chromosomes respectively. In the 46 chromosome type complete sterility was found. At diakinesis there were 18 bivalents and 10 lagging univalents. Presumably these 10 were maize chromosomes, the bivalents resulting from the pairing of the *Tripsacum* chromosomes *inter se*.

In the 28 chromosome types, there is complete lack of pairing between the 10 *Zea* and the 18 *Tripsacum* chromosomes, resulting in marked irregularity in gametic numbers. As a consequence the hybrid is completely pollen sterile, but partially fertile when back-crossed by either of its parents, giving 3.4 per cent. with *Zea* and 1.3 per cent. with *Tripsacum*. This is due to the fact that occasionally

all the chromosomes pass to one nucleus, and at the second division gametes form with a complete set of both *Tripsacum* and *Zea* chromosomes. In the back-cross with *Zea*, all the hybrids had 38 chromosomes, 18 presumably being *Tripsacum* chromosomes, and 20 *Zea* chromosomes.

In view of the fact that the *Zea-Tripsacum* hybrids very occasionally produced gametes with both the genomes of the parents, Mangelsdorf and Reeves (1931) pollinated the hybrid with pollen from *Euchlaena mexicana*. The fertility was fairly high—seed set to the extent of 5.8 per cent. They thus produce a tri-genom hybrid with 38 chromosomes. (*Zea* 10 + *Tripsacum*, 18 + *Euchlaena* 10.) The hybrid was very markedly sterile. Since, however, *Euchlaena* chromosomes are known to pair with *Zea* chromosomes, it was anticipated that at meiosis the hybrid would exhibit 10 bivalents plus 18 univalents. This was found to be the position. There were 10 bivalents showing regular segregation, and 18 univalents exhibiting random segregation.

The phenotype of this hybrid is discussed in the section on the origin of maize. (See pages 465-9.)

The reciprocal crosses failed. Annual Teosinté, however, produced shrivelled seed when pollinated with *Tripsacum* pollen. These results are at variance with the earlier results obtained by Collins and Kempton (1916).

**ECONOMIC USES OF MAIZE.**—No other plant has been put to such diversified uses. The whole plant may be used as fodder or ensilage. The whole ears or the shelled grain, the latter often after soaking, or partial cooking, may be fed to stock. The crushed embryo and the bran are utilized as the basis of several cattle cakes.

The milling products are almost endless. The grains may be ground as such. More often, the grain products are separated—bran, embryo and flours. The flours are prepared in various grades, from the coarser "hominys" to the creamy "corn flour". "Sweet Corn" is now a recognized "vegetable", and—inevitably—canned for all the year round use. "Pop corns" are not only "popped", but disguised in many other forms.

Maize—especially in the United States—is one of the main sources of starch. From the starch, by partial hydrolysis, "corn syrup" is produced—a mixture of glucose and dextrines. It is used not only as a food substance, but in the manufacture of soap, caramels, chewing gums, leather, etc.

The dextrines obtained are used as adhesives, as size for paper and cloth, and as glaze for rice and coffee. "Corn sugar" is the ultimate product of complete hydrolysis. It consists of almost pure glucose.

The expressed oil from the germs is put to many uses. Purified, it is used for culinary purposes and, after being hydrogenated, as a lard substitute. The cruder oil may be vulcanized to form a rubber substitute; or used in the manufacture of glycerine, soaps, paints, varnishes and certain oil-cloths.

The grains as well as other parts of the plant may be fermented, producing acetic acid and alcohol. Fermentation by *B. amylobacter*, yielding butanol and acetone, is now being exploited. The pith of the stems is a useful source of almost pure cellulose. The larger cobs are used for the making of pipe-bowls; and the husks have been employed in the making of hats, rugs, and even paper.

ORIGIN OF MAIZE.—Maize, cultivated since pre-historic times, is unknown in the wild state. Further, the earliest varieties discovered are essentially similar to the modern.

In spite of statements to the contrary, de Candolle (1881) concluded that maize was not a native of the Old World and that it "became rapidly diffused after the discovery of America". Further, "At the time of the New World, maize



FIG. 188.—"Ears" of the trigeneric hybrid, *Zea*, *Tripsacum* and *Euchlaena*. (After Mangelsdorf and Reeves, by permission of the J. of Heredity.)

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was one of the staples of its agriculture from the La Plata valley to the United States." (See Kempton, "Maize and Man". Reprint J. of Heredity.)

Recent investigations by the Russian expedition to Central and South America under the direction of Bukasov (1930) enables us to visualize the distribution. Kuleshov's analysis of the material so obtained indicates the following centres of diversity :

(1) *Amylacea*—the soft maize—with its centre in Columbia and Peru ; (2) *Indurata*—the flint maize—in Central America ; (3) *Indentata*—the dent maize—and *everta*—the pop maize—in Central Mexico. No material of *Saccharata*—sweet maize—nor of *tunicata*—pod maize—was found in Mexico, though others have stated that *saccharata* occurs there. Kuleshov further regards the *amylacea* group as the most primitive and, if this be accepted, the main centre of origin must be regarded as the plateau of Bagota in Peru, which coincides very closely with de Candolle's early deduction.\*

Two American genera are closely related to *Zea*—*Tripsacum* and *Euchlaena*. The genus *Tripsacum* has three representatives in North America, the best known being *Tripsacum dactyloides* L. It is a tufted perennial grass with well-developed root stocks and leaves very much narrower than those of *Euchlaena* and *Zea*. The inflorescence is a simplified huskless panicle with two to three more or less equivalent branches, carrying both staminate and pistillate spikelets. The pistillate spikelets are few in number (average—18) and are situated at the base of the inflorescence : the staminate spikelets are much more numerous (200 to 400 in number) and are situated in pairs over the whole length of the rachis with the exception of the base. At maturity, the rachis is brittle and as in *Euchlaena*, the seeds are enclosed in a brittle shell. (See Fig. 186.)

According to Longley (1924) *T. dactyloides* has 70 somatic chromosomes, but Avdulov (1931) maintained that it had not less than 72 and probably as many as 80. Other investigators have found the number to be 36. It is therefore probable that there are both diploid and tetraploid strains. Thus Mangelsdorf and Reeves (1931) in crossing *Zea* and *Tripsacum* used two forms of *Tripsacum*—a Connecticut strain with 72 chromosomes and a Texas strain with 36. The basic chromosome number in the genus is therefore different from that of *Zea* and *Euchlaena* (10).

The second genus, *Euchlaena*, has two representatives in Mexico ; *Euchlaena Mexicana* Schrad., and *Euchlaena perennis* Hitch. Both species are practically identical morphologically, but *Eu. Mexicana* is annual with 20 somatic chromosomes and *Eu. perennis* perennial with 40 somatic chromosomes. In all probability the latter species is a tetraploid derived from *Eu. Mexicana*.†

*Euchlaena Mexicana* (Teosinté) may be found growing as a weed in maize fields in Central America and natural hybrids between the two are now known to occur. It is much more maize-like in habit than *Tripsacum*, but produces a considerable number of basal tillers or suckers. The leaves too are somewhat

\* See also Kožukhov, I. v., 1935 ; Bull. Appl. Bot. Leningrad. Ser. A (16) : 5-18.

† Longley (Morphological characters of Teosinté chromosomes, (J. Agr. Res. 54 : 835-862 ; 1937) has demonstrated the presence of knobs on the chromosomes of Teosinté and *Tripsacum*. These knobs are similar to those found in Maize. In *Tripsacum* they are all terminal : in Teosinté they may be terminal only or both terminal and internal. In the types studied, the position of a knob on any one chromosome was constant.



narrower. As in maize, the staminate spikelets are confined to the terminal tassel whilst the pistillate spikelets are situated on short lateral spikes which are enclosed in husks. The tassels, however, are shorter than those of maize, and consist of a number of more or less equivalent branches diverging from the main axis almost simultaneously; no central spike can be distinguished. Each branch of the tassel bears a very large number of spikelets, which are arranged in pairs (as in maize), one sessile the other pedicelled. (See Figs. 185; 189 (D) and 190 (C).)

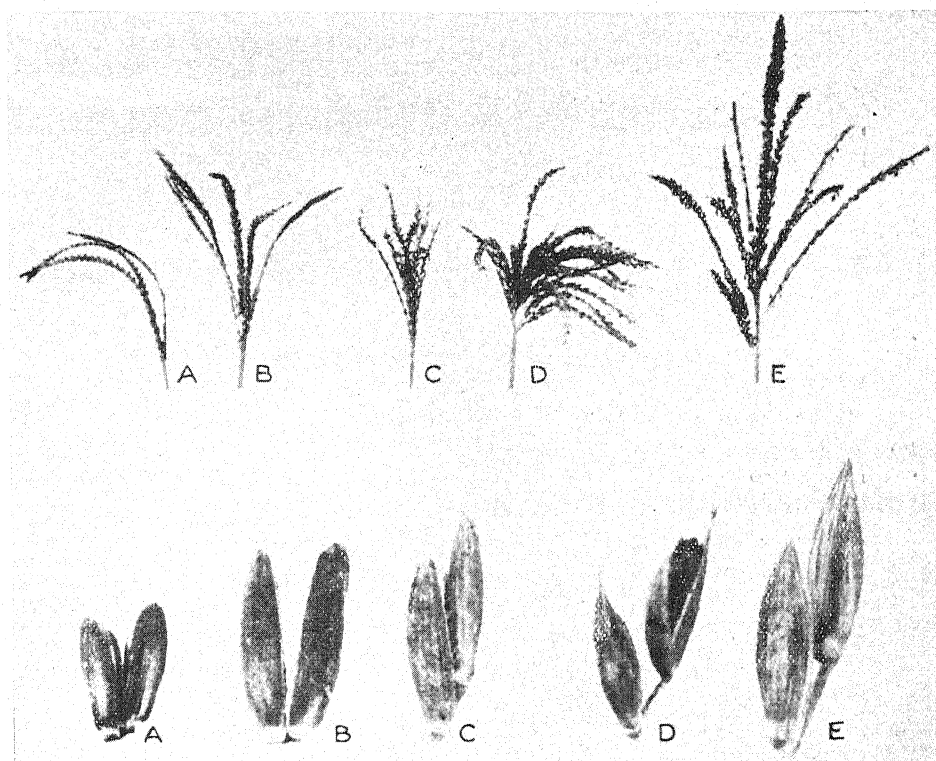


FIG. 189.—Tassels and "Male" spikelets of the trigeneric hybrid and its parents.  
Upper row : The Tassels.  
Lower row : The male spikelets.  
A. *Tripsacum*; B. *Zea* × *Tripsacum*; C. *Zea* × *Tripsacum* × *Euchlaena*; D. *Euchlaena*; E. *Zea*. (After Mangelsdorf and Reeves, by permission of the J. of Heredity.)

The pistillate spikes are very different from those of maize. They are numerous, husked and short with the spikelets in two sessile rows on a brittle rachis. The flowers, however, resemble maize in having a long practically undivided "silk".

At maturity the grains are enclosed in an indurated husk, the product of the glumes and a portion of the rachis.

Comparing the three genera, it is obvious that *Euchlaena* and *Zea* are more nearly related to one another than either to *Tripsacum*. The fact that *Zea* and

*Euchlaena* cross very readily and that the hybrids are fertile with normal meiosis indicates that their chromosomes are markedly homologous. This homology is substantiated by the recent evidence that their chromosomes carry certain allelomorphic genes. Nevertheless, the differences between the two are such that

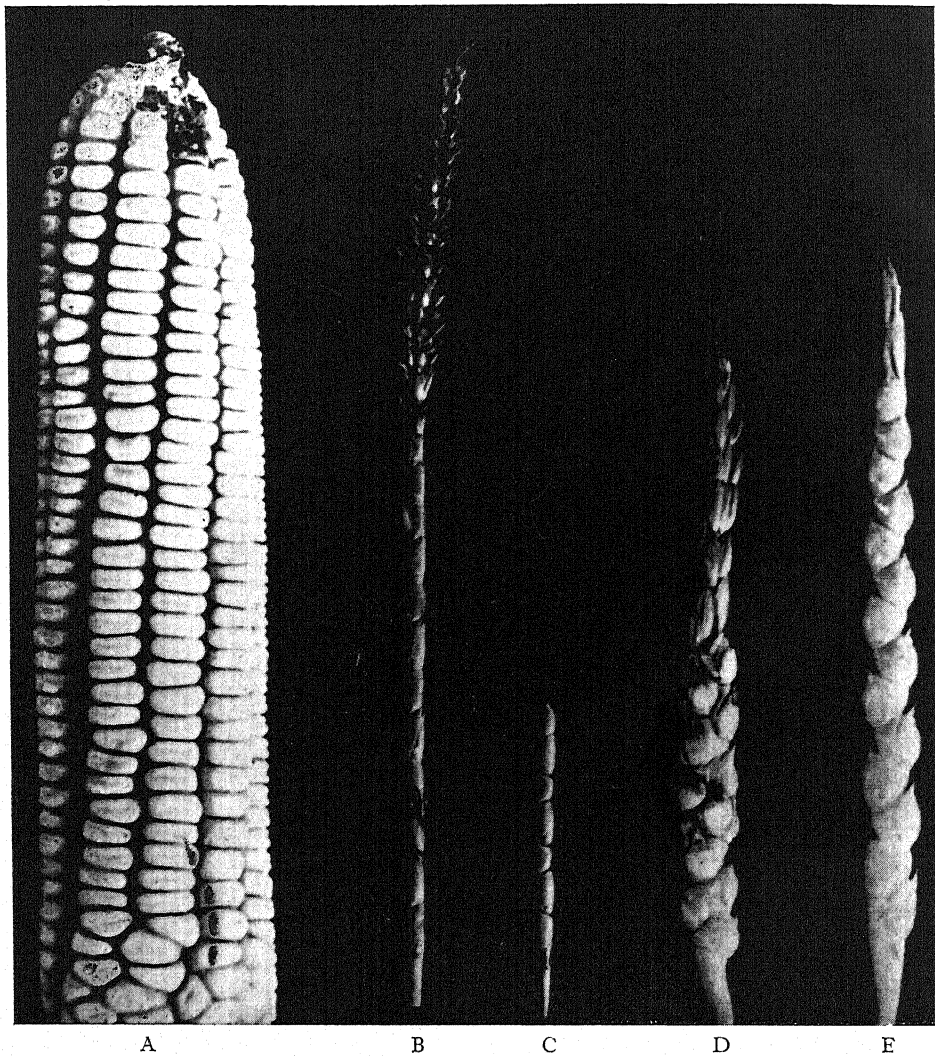


FIG. 190.—Pistillate spikes of trigeneric hybrid and its parents.

A. *Zea*; B. *Tripsacum*; C. *Euchlaena*; D. *Zea* × *Tripsacum*; E. *Zea* × *Tripsacum* × *Euchlaena*. (After Mangelsdorf and Reeves, by permission of the J. of Heredity.)

it is impossible that the highly specialized *Zea* arose from the equally specialized *Euchlaena*. Further, as Collins has put it "any plant with the characters of *Euchlaena* would be most unpromising material from which to develop a good food plant".

Some 30 years ago there was discovered a so-called "wild maize" with several primitive characteristics. On analysis it proved to be of hybrid origin, the result of back-crossing with maize, a hybrid of maize and Teosinté. Such hybrids as already noted occur naturally in Mexico. This discovery led to much speculation. It was argued that maize must be of hybrid origin, the result of inter-crossing Teosinté with some other grass. This is a possibility, but no one has been able to say what this unknown grass was, nor what were its characters.

Most writers in recent years have adopted the theory that the American genera *Zea*, *Euchlaena* and *Tripsacum*—all highly specialized types—have evolved independently from a common extinct ancestor or closely allied ancestors.

Various attempts have been made to picture this ancestral form. The last of these imaginary pictures, based on taxonomic and morphological grounds (Weatherwax, 1935) bears a close resemblance to the trigeneric hybrid obtained by Mangelsdorf and Reeves, and here figured. (See Figs. 188; 189; 190.)

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